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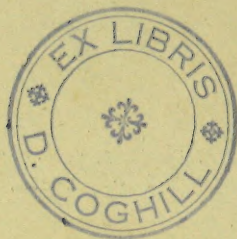
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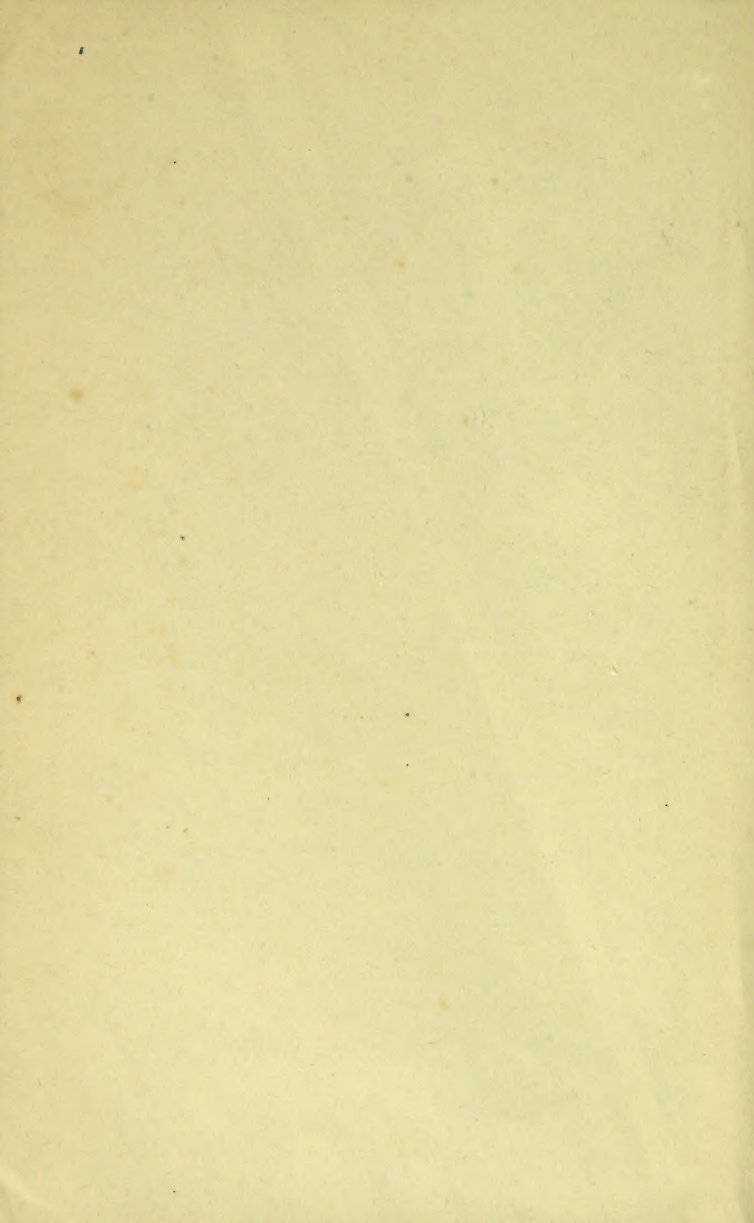
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Laboratory of Physical Biology



THE ANATOMY,  
PHYSIOLOGY, MORPHOLOGY,  
AND DEVELOPMENT  
OF  
THE BLOW-FLY.

(CALLIPHORA ERYTHROCEPHALA.)

A Study in the Comparative Anatomy and Morphology of Insects.

*WITH PLATES AND ILLUSTRATIONS EXECUTED DIRECTLY FROM  
THE DRAWINGS OF THE AUTHOR.*

BY

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## P R E F A C E .

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IN 1870 I published a small treatise on the 'Anatomy of the Blow-Fly.' This has now been out of print for nearly ten years. In 1890, when I undertook the present work, a book of about 300 pages was contemplated ; since then, however, it has grown to more than twice that size, and it has been found necessary to divide it into two volumes.

The present volume deals with the subject generally—with the anatomy of the larva and the development of the embryo in the egg and of the nymph in the pupa, as well as with the external skeleton and histology of the perfect insect. The second volume will consist of a detailed description of the various internal organs, their development and physiology. The issue of the parts of this volume has been unavoidably delayed. The introduction and the first four chapters appeared in October, 1890, the fifth chapter in April, 1891, and the remainder in April, 1892.

It is hardly to be expected that a work of the present magnitude can be without errors, but I trust that any which may be found will be unimportant. I have endeavoured to keep matters of fact distinct from the hypotheses and conclusions

which rest upon them. Many of my views are diametrically opposed to those usually received. In such cases the accepted view has been given as well as my own.

Every student will acknowledge that the morphology of Arthropods has made immaterial advances during the past fifty years when compared with that of Vertebrates; yet an immense number of new observations have been recorded. This is sufficiently proved by the enormously increased literature upon the subject.

I have availed myself largely of this accumulated literature, but I have never allowed myself to be guided by mere text-book statements, unless these on investigation have been found consistent with my own observations. Many may possibly depreciate my want of faith in statements which have been repeated until they appear to be almost incontrovertible; but I am content to await the verdict of posterity on my conclusions. Some of my views will, of course, be replaced by others, but I have the strongest belief that most of them will withstand adverse criticism, and will ultimately be accepted. If this is so, many of the old statements will disappear from future text-books as completely as the Vertebrate morphology of fifty years ago has vanished from those of to-day.

## INTRODUCTION.

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ALTHOUGH the study of the anatomy of insects was formerly cultivated with great assiduity by such men as Swammerdam, Malpighi, Lyonet, Straus Durckheim, and more recently by Leydig, it is a science which has never found a home in England; moreover, the improvements in the compound microscope, which have made a new epoch in biological studies, have rather checked than advanced the study of insect anatomy, by diverting investigation into what appeared for a time more fertile fields of research. In the last twenty years, however, many remarkable monographs have appeared in France, Germany, and Russia, and our knowledge has been greatly advanced; yet, extraordinary as it may appear, there is no really competent treatise on insect anatomy, in English, of more recent date than Newport's article 'Insecta' in Todd's Cyclopædia (1836). If we wish to make ourselves acquainted with the researches of late years, it is necessary to consult many memoirs in several languages—Graber's work, 'Die Insecten,' to a certain extent, is available to those conversant with German, and Miall and Denny have given us an excellent memoir on the cockroach, which is, however, insufficient as an

introduction to the study of so highly modified a type as the Blow-fly. I have therefore followed the example of Straus Durckheim, and given a *résumé* of the principles of anatomy, morphology, and histology, applied to insects generally in a series of introductory chapters and sections, in order that the most recent knowledge collected by many observers may be presented to my readers, and enable them to understand more completely the characteristic peculiarities of the very remarkable type I propose to describe, and its relations to other forms of insect life.

The term 'Blow-fly' is applied indiscriminately, not only to several species of a single genus, but to those of other genera and sub-genera. My own researches, which have extended over nearly a quarter of a century, have been chiefly made upon the most abundant form in this country, *Calliphora erythrocephala*, and when I speak of the Blow-fly in the following pages, unless otherwise stated, my observations refer to this species only.

During the past two years most of my researches have been made in my new laboratory at the Middlesex Hospital Medical School. I am indebted to my Demonstrator, Mr. G. C. Karop, for valuable help, and more especially for the trouble he has taken in correcting my proofs, and to Mr. A. W. Kappel, the sub-librarian of the Linnean Society, for the zeal he has shown in searching out and obtaining for me many of the works I have consulted.

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## ERRATA.

Page 17, line 8, *for* 'hypoblast behind,' *read* 'hypoblast behind the blastopore.'

Page 33, last line, *for* 'xvi.' *read* 'xiv.'

Page 65, in footnote, *for* 'K. L. C.' *read* 'C. L. C.'

Page 77, in footnote, *for* 'Chironomus' *read* 'Corethra.'

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## CHAPTER I.

### THE LIFE-HISTORY OF THE BLOW-FLY.

THE life-history of the blow-fly may be conveniently divided into four stages; (1) the egg; (2) the larva; (3) the pupa, and (4) the imago states.

**The Egg.**—The female insect deposits her eggs in packets on those parts of dead birds or animals which are not covered by hair or feathers, or upon raw or even cooked meat; and occasionally, it is said, upon the fleshy petals of certain plants (*Stapelia*, etc.) which have a carrion-like smell. The number of eggs in each packet varies between three or four and a hundred or more.

The eggs are usually fecundated at the moment of deposition, and the larva effects its escape from the egg in from twenty to twenty-four hours.

At the end of the first twelve hours the embryo already possesses a rudimentary head with all those parts usually found in insects at a corresponding period of development.

**Bibliography.**—In this and the following bibliographies it has not been my intention to include every book upon the subject, but only those to which I am indebted, or which possess historic interest and contain original work. The numerals prefixed are given in the text thus [8], when a work is quoted or referred to, and are consecutive.

1. REAUMUR, DE, 'Mémoires pour servir à l'Histoire des Insectes,' 4to., tom. iv., Paris, 1738.

The fourth and seventh Mém. are in part devoted to the life-history of the blow-fly, and are exceedingly interesting.

2. WEISMANN, A., 'Entwicklung der Dipteren.' Leipzig, 1864. Also in *Zeitsch. f. wissensch. Zool.*, Bd. xiii. and xiv. 1863-64.
3. GLEICHEN, W. F. F., 'Geschichte der gemeinen Stubenfliege' (The House-fly). Nürnberg, 1790.

Is interesting on account of its antiquity, and gives an account of the life-history of the house-fly.

During the remainder of the embryonic stage all the changes which occur are apparently retrogressive. The head is in great part withdrawn into the interior of the embryo, so that when the maggot emerges from the egg, the parts destined to form the head in the perfect insect are found deeply invaginated, and lie far back in the thoracic region, in front of the highly concentrated nervous system.

The newly-hatched larva buries itself in the carrion on which the eggs are deposited, and feeds continuously for fourteen days, by which time it has attained its full growth. I believe in warm weather this period is considerably shortened, and that the full growth of the larva is attained in eight to ten days, but the time necessary evidently varies with the temperature and with the condition and nature of the food, and it has been differently estimated by several writers. It is shorter in *Musca cæsar* and *Sarcophaga carnaria*. The newly-hatched larva measures nearly 2 mm., or  $1\frac{1}{2}$  in., in length when fully extended. It sheds its cuticular integument within two hours after its escape from the egg, and I have actually observed this first moult in larvæ hatched in a watch-glass. A change occurs in the form of the mouth armature and the structure of the posterior spiracles at the first moult. As a pair of anterior spiracles are subsequently formed, and further changes occur in the mouth organs and posterior spiracles, it must be inferred that other moults occur, but their number is unknown, as the newly-hatched maggot immediately buries itself in its food. Weismann concluded that the larva undergoes at least three. Burmeister [8] erroneously supposed that no moults occur in the larvæ of the Muscidæ.

The full-grown larva when it ceases to feed measures  $\frac{2}{3}$  of an inch in length when fully extended, and weighs 10 to 12 centigrammes, or about 1.5 grains. It leaves the carrion in which it has been nourished and buries itself in the earth. It is not immediately transformed into a pupa, but becomes a resting larva.

**The Resting Larva.**—The duration of the resting period varies greatly with the temperature: it may not exceed two days, and may extend to several weeks or even months.

When the larva ceases to feed its crop is greatly distended, but during the resting period it is gradually emptied with the rest of the alimentary canal; the head is withdrawn within the second annulus, and the whole worm is contracted, and assumes an ovoid form. If disturbed, the head is protruded, and the larva crawls about rapidly, seeking to bury itself again; after a variable period, however, the contraction of the body becomes permanent, all power of movement is lost owing to the inner layer of the integument and the muscles of the larva having detached themselves from the external cuticle: this is the commencement of the pupa state.

It has long been known that a number of curious cellular bodies exist connected with the nerves and nerve centres of the larva. These were formerly regarded as ganglia, but Dr. Weismann [2] discovered their true nature. They are the rudiments of the fly; he named them *imaginal discs*. It has also been suggested that the largest of these imaginal discs is the invaginated portion of the head of the embryo. Quite recently I was fortunate enough to make longitudinal sections of a newly-hatched larva, which not only demonstrate the fact, but also show the exact nature of the invagination (see Chap. IV., Sec. 3, Fig. 7).

During the resting stage two processes are going on simultaneously, the various larval organs are undergoing rapid disintegration, and the imaginal discs are unfolding and increasing in size and complexity.

**The Pupa Stage.**—In warm weather at the end of two, or at most three days, and in cold weather often after the lapse of several weeks or months, the integument of the contracted larva undergoes a change of colour and texture. At first it turns yellow, then red, and finally black, and with this last change it also becomes hard and brittle; the insect is now a pupa.

The four anterior rings of the pupa-case are separated from those behind by a seam or *raphé*, and are readily detached as a cap in the fully-formed pupa. It is by this means the imago, or perfect insect, escapes from the pupa-case.

If the pupa-case be opened just before it becomes black,

it will be found to contain nothing apparently but a white cream-like fluid; but on careful microscopic examination some of the imaginal discs will be detected, and many of the muscles of the larva still remain at its posterior end. The imaginal discs are really very numerous; fourteen were known to Weismann, and about fifty have been discovered since, besides many scattered groups of cells (*histoblasts*), from which the internal organs originate; so that there are in all more than sixty separate discs, which subsequently unite with each other, and form the embryonic fly within the pupa-case. This embryonic fly is known as the nymph.

**The Nymph** corresponds with the chrysalis of a lepidopterous insect, and has its wings, legs, and proboscis folded mummy-fashion over its ventral surface.

It is entirely formed from the imaginal discs. All the organs of the larva, without exception, undergo disintegration, and are converted into a creamy fluid—the pseudo-yolk, by which the imaginal discs are nourished.

The nymph is also developed in a very peculiar manner. Its head is at first enclosed within its thorax, and its thorax is enclosed within its abdomen. Subsequently, the abdomen is drawn back, exposing the thorax, and the thorax is drawn back, exposing the head.

**The Imago**, or perfect insect, is the fully developed nymph, and escapes from the pupa-case at the end of from twelve to fourteen days in summer; but in winter the pupa stage may last for months, as all development is arrested by a temperature below 45° Fahr. The preservation of the species in winter depends mainly upon this circumstance. The fly escapes from the pupa-case by pushing off the operculum, or cap. This is effected by the distension of a large bladder-like organ on the insect's forehead—the frontal sac. When it first emerges it is of a pale ash-gray colour, and very soft; its wings are moist, thick, and crumpled, and the large frontal sac projects from its forehead. The proboscis and many of the internal organs are in a half-developed condition. In two or three hours the newly-escaped insect, which rapidly increases in size by dis-

tending its respiratory sacs with air, assumes a dark colour, and its integument becomes hard and elastic. Its wings are fully developed, and it rises in the air and takes its first flight.

By this time the frontal sac is permanently withdrawn into the head, and the external form, characteristic of the mature insect, is attained. There are still, however, traces of immaturity in the coloration of the integument, and the imperfect hardening of the head and thorax, which is not complete for several days.

A few hours appear to suffice for the full sexual development of the male, though three or four weeks are needed for that of the female—a condition which probably prevents the fertilization of females by males of the same brood.

The female may lay several hundred eggs, but these cannot all be deposited at the same time, as the ovaries contain four or five sets in different stages of development. About 180 eggs are matured at one time, three or four times as many remaining in a rudimentary condition.

The female is fecundated but once; the eggs are usually fertilized as they are deposited; but two, or possibly three, fertilized eggs may be retained in the oviduct, so that under exceptional circumstances one or more living larvæ may be deposited by the female fly.

Many species of allied genera normally retain the fertilized eggs in a special ovisac until they hatch, and living larvæ are deposited instead of eggs. *Sarcophaga*, *Scatophaga*, and *Tachina* are examples of such viviparous flies.

The female blow-fly usually exercises discrimination in the deposition of her eggs, and the number laid apparently bears a proportion to the mass of carrion. I have repeatedly seen these insects examining a portion of flesh on all sides, and if eggs in sufficient number are already there, rejecting it as unsuitable for their purpose. The males seldom enter houses except in cold weather, and are usually found on flowers; inseminated females frequent carrion and are found in houses; but those with ripe eggs are seldom seen in

our dwellings until late in autumn, although they abound in butchers' shops, slaughter-houses, and similar places.

The question of hibernation is a difficult one to settle. All 'winter flies' are, I believe, immature, as I have never found one with ripe eggs; still, I strongly suspect mature females hibernate occasionally.

In the winter of 1889 I had a bell-glass in my laboratory full of immature blow-flies, which had recently issued from the pupæ. One very cold morning when I went in not a fly was to be seen. I imagined the bell-glass had been lifted, and that my flies had escaped. On closer investigation, however, I discovered them all closely huddled together in a hollow under the base of a cup containing pupæ. The cup had been slightly tilted, and every insect had retreated into this narrow space. As soon as the temperature of the room rose to 55° Fahr., the insects emerged from their concealment, and were as lively as ever.



THE FLESH-FLY.  
(*Sarcophaga carnaria*.)

## CHAPTER II.

### AN INTRODUCTION TO THE STUDY OF THE ANATOMY AND MORPHOLOGY OF INSECTS.

THE body in all insects may be regarded as a simple thick-walled tube, the cavity of which forms the alimentary canal. There is no distinct continuous body-cavity, in which the viscera lie, corresponding to the pleuro-peritoneum of a vertebrate, or the continuous cœlom of a hollow-bodied worm (nematoid); but all the organs are connected together by a delicate sustentacular tissue, formed of branching cells, in the

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**Bibliography.**—The general subject of insect anatomy and morphology.

4. SWAMMERDAM, 'Bybel der Natuure.' Utrecht, 1669; Leyden, in Latin and Dutch, Boerhaave's edition, 1738; and Leipzig, 1752.

5. REAUMUR, DE, 'Mémoires pour servir à l'Histoire des Insectes.' Paris, 1734-42, 4to.

6. DE GEER, 'Mémoires pour servir à l'Histoire des Insectes.' 4to, Stockholm, 1752-78.

Not an anatomical work in any sense, but often quoted; a treatise on systematic entomology.

7. FABRICIUS, J. C., 'Philosophia Entomologica.' Hamburgi et Kilonii, 1778.

A curious little book, which is useful in regard to nomenclature of parts, but of no use as a treatise on structure. His 'Systema Entomologia,' Flensburgi et Lipsiæ, 1775, is a work on systematic entomology.

8. BURMEISTER, 'Handbuch der Entomologie.' Berlin, 1832, 8vo.

Translated into English by Shuckard, with additions by the author and original notes by the translator. London, 1836, 8vo.

9. NEWPORT, G., Article 'Insecta,' Todd's 'Cyclopædia of Anatomy and Phvsiology,' 1836-39. London.

Still the best work in English on insect anatomy.

10. GRABER, V., 'Die Insecten.' Munich, 1877, small 8vo.

The best account of the anatomy and development of insects in a popular form.

meshes of which the blood circulates, although there are special cavities, blood, or more properly lymph, sinuses in various parts of the body. The blood of insects is in fact equivalent to the lymph of vertebrates, which it closely resembles in its physical and microscopic characters.

The somatic nervous system\* consists of two parts—a cephalic nerve-centre or brain, which lies in front of the mouth; and a double ganglionated cord, which is situated on the ventral aspect of the alimentary canal. The dorsal vessel, or heart, is placed immediately beneath the skin of the back, hence the ventral aspect is known as the neural, and the dorsal as the hæmal surface of the animal.

The whole body is segmented transversely into a number of annuli or somites, and these are grouped, in the adult form or imago, into three distinct regions, known respectively as the head, thorax, and abdomen.

The somites of the head and thorax usually each possess a pair of ventral appendages, jaws or limbs, and one or two of the thoracic somites are generally provided with dorsal appendages—wings. A somite with its appendages is spoken of as a metamere; the terms ‘somite’ and ‘metamere’ are synonymous when all appendages are wanting.

The external surface of the body is covered and protected by a cuticle, impregnated more or less completely by a horny substance called chitin, which renders it very dense and elastic, and usually forms a complex exoskeleton. The cuticle often consists of many super-imposed laminæ, and is formed by an underlying layer of cells known as the hypodermis, which represents the external cellular epithelium of the mollusca and the vertebrata, and which corresponds with the epiblast of the embryo (see Fig. 1).

The cells of the hypodermis are usually short hexagonal prisms, cemented together by their edges. In the larva the size of these cells increases with its growth, and in the adult larva they are generally very much larger than the correspond-

\* See Chap. IV., Sec. 7.

ing cells of the nymph or imago—at least, in the metabola and hemi-metabola.

Chitin is a nitrogenous substance more nearly related to mucin than to any other substance found in vertebrates. The large hypodermic cells of many larvæ exhibit cup-shaped cavities on their outer surface, which present a great similarity to those of the well-known goblet cells of the mucous membranes. Latreille regarded chitin as the result of the degeneration of the external portion of the cell-substance

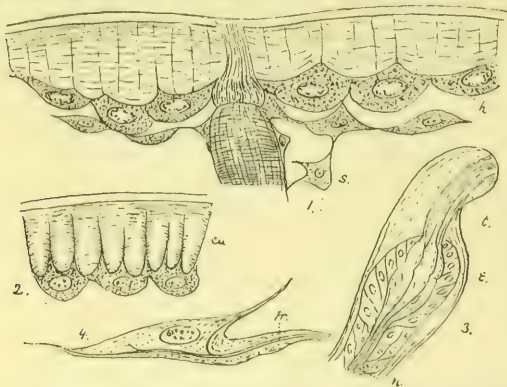


FIG. 1.—Sections of the skin of the Blow-fly larva.—1, a vertical section showing the hypodermis *h*, with the super-imposed cuticular layers; 2, a similar section, showing the cuticular prisms; 3, a sensory papilla; 4, a sub-hypodermic cell. *cu*, Cuticle; *c*, nerve end organ; *t*, terminal portion of the end organ; *n*, nerve; *s*, sub-hypodermic tissue; *tr*, trachea.

[9, p. 882], a view in which I must concur. Chitin is very insoluble in solutions of the caustic alkalis, a property which enables the microscopist to make beautiful preparations of the exo- and endo-skeletons of insects.

The cuticle consists of two distinct parts, which correspond with the epiostracum and endostracum of the Crustacea.\* I shall, therefore, use these terms to distinguish them.

\* Huxley, T. H., 'The Crayfish.' London, 1880, p. 192.

The **Epiostracum** consists of a single external lamina, which differs considerably from the rest of the cuticle in the readiness with which it takes stains. It is apparently quite structureless, or is divided into hexagonal fields.

The **Endostracum** is formed of numerous lamellæ, except in the hard plates of the exo-skeleton, which do not usually exhibit a laminated structure. It is often divided by vertical planes into hexagonal prisms, several corresponding to a single hypodermic cell. In the imago, when it first emerges, the endostracum is not usually present except where sclerites are already developed.

**Sclerites.**—This term is applied to the denser cuticular structures which form the exo-skeleton. The hardness and thickness of the several parts of the cuticle are by no means in direct relation to each other. The denser plates are usually thinner than the membranous parts of the cuticle between them. Thus in the imago of the blow-fly the hardest dermal plates vary from  $10^{\mu}$  to  $20^{\mu}$  in thickness, whilst that of the intervening integument in some parts is  $100^{\mu}$ . The flexible portions of the integument are usually transparent and colourless, whilst the sclerites are deeply pigmented and opaque.

**Syndesmotic Membrane.**—The soft flexible cuticle between the sclerites has been termed conjunctiva, but, as the articulations which it forms are known as syndesmoses, I shall prefer the term syndesmotic membrane.

**Scales, Setæ, and Vibrissæ** are solid or hollow projections of the cuticle. The large scales and setæ are hollow, with a giant cell beneath each, the trichogenic cell. It gives off a process which fills the interior of the hair or scale.

The large scales and setæ are usually articulated with the cuticle of the surface, which forms a kind of socket around the opening or foramen, through which the process of the trichogenic cell enters the seta.

The smallest setæ are solid, the larger ones are ribbed; some are deeply channelled on one side.

The larger bristles (setæ) of the Diptera are remarkably persistent in number and position throughout very large families. Osten-Sacken regards their arrangement, *chatotaxy*,

as important in relation to classification.\* The very early development of the setæ in the nymph is an indication in favour of his view.

The Diptera generally, and the Muscidæ more especially, exhibit two very distinct modifications, which Osten-Sacken calls the Diptera chætophora and the Diptera cremocheta. The former are densely covered with bristles, and use their legs to run, climb, and snatch their prey; their flight is headlong, and they rarely or never poise over flowers. The olfactory sense appears to predominate. On the other hand, the latter hover and poise on the wing. They are smooth and have no bristles, or very few. Many are brightly coloured. The visual sense appears to predominate, and they only use their legs to alight and when resting. They are helpless in the dark, and are seldom abroad except on sunny days. Dr. A. Forel† says that 'insects organized for an exclusively aerial life depend on their eyes. They generally have little developed antennæ, and are absolutely helpless in the dark; they hardly dare to walk. . . . In other insects the eyes play a very subordinate part. These may be called antennal insects. They can work by night or underground as well as by day.'

The blow-fly belongs to the chætophorous division, and is in some degree an antennal insect in Forel's sense, but it has evidently good visual powers.

**Apodemes** are rod-like involutions of the cuticle, to which muscles are attached. They are frequently very strong, and act as powerful levers.

The **Thorax** in the imago is always provided with three pairs of jointed limbs. The anterior pair are sometimes rudimentary. It consists entirely or in great part of three metameres, known respectively as the prothorax, the mesothorax, and the metathorax.

**Tracheæ.**—Insects always possess a peculiar respiratory

\* Osten-Sacken, C. R., 'An Essay on Comparative Chætotaxy.' Trans. Entom. Soc., London, 1884. Originally printed in Mitth. der Münchener Entom. Vereins, Bd. v., 1881.

† A. Forel, 'Beitrag z. Kenntniss der Sinnesempfindung der Insecten.' Mitth. d. Münchener Entom. Vereins, ii., 1878.

system, consisting of branching tubes called tracheæ. These usually open externally by a series of lateral spiracles, or breathing pores, on or between the obvious segments of the thorax and abdomen. Even when spiracles are absent and the tracheæ exhibit no external opening, these tubes are always found filled with air.

Insects have been defined as arthropods, or animals with jointed limbs, with a distinct head, thorax and abdomen, and a respiratory system consisting of tracheal vessels.

**Morphology**, or the relation of the various parts of the body to each other and to the corresponding parts of other animals, forms the basis of all scientific anatomical nomenclature. Without a knowledge of these relations all nomenclature would be uncertain and arbitrary. Without such knowledge each author would give an organ or part a name, one name would be as good as another, and inextricable confusion would result. All sound morphology depends upon a study of the developmental process.

In insects development is often discontinuous, progresses rapidly in the egg to a certain stage, and then suddenly ceases, or appears to retrogress. After a longer or shorter period of growth it recommences, and gives rise to remarkable metamorphoses. Development in the egg is spoken of as embryology; that of metamorphosis, as after-development (*nach-embryologie*).

**Embryology**.—The ovum of an insect consists of a germ and a vitellus, or food-yolk. The relation of the germ to the vitellus has long been a problem awaiting solution.\*

The germ consists of a germinal vesicle and a germinal spot. It corresponds to the cicatrix of the bird's egg; the vitellus also corresponds to the yolk of the egg in birds and reptiles. The egg is enclosed in two membranes—an external shell or chorion, and a thin internal membrane, the yolk sac or vitelline membrane. These, like the shell and vitelline membrane of the bird's egg, take no part in the formation of the embryo; their function is merely protective.

\* Balfour, 'Comparative Embryology,' 1881.

**Yolk Cleavage.**—In the animal kingdom generally, the first change which occurs after impregnation is the division of the germ, first into two, and afterwards into four, eight, and sixteen, cells. This subdivision continues until a cellular membrane, the blastoderm, is completed. When a food-yolk is present this also undergoes more or less complete segmentation, forming what are known as yolk spherules.

In insects the segmentation of the food-yolk commences in its interior. This form of segmentation is known as centrolecithal. It appears to be characteristic of all arthropods.

The **Embryo** is developed from the blastoderm, which entirely surrounds the yolk at a very early period. It consists at first of a single layer of cells, but afterwards of three distinct layers. The most external of these is the epiblast, the innermost is the hypoblast, and the intermediate layer is the mesoblast.

The hypoblast encloses a cavity known as the archenteron, and at a later period of development as the mesenteron.

Recent observations made by Bütschli\* and by myself on the fly embryo have shown that the hypoblast and epiblast are at first continuous, and that the archenteron is formed by a dorsal invagination, which opens externally on the dorsal surface of the embryo by a large blastopore (Fig. 2, between *dp* and *h*).

The first traces of an embryo as distinguished from the blastoderm appear as a shallow pit on the ventral surface of the blastoderm, the primitive mouth or stomodæum, and as a narrow, somewhat opaque, longitudinal streak behind it—the primitive band.

The primitive band arises from the multiplication of the embryonal cells on the inner surface of the epiblast; it is distinctly divided into two lateral halves by a median furrow. A second pit soon appears at the posterior end of the primitive band; it is the proctodæum, and becomes the rectum.

The stomodæum becomes deeper as development progresses, and ultimately forms a blind tube, which becomes the fore-gut.

\* Bütschli, 'Gegenbaur. Morph. Jahrbuch,' 1888, p. 170. With figures.

Its closed end comes into contact with, and is afterwards invaginated in, the anterior extremity of the mesenteron, as the archenteron is designated after the closure of the blastopore.

Similar changes also occur in the proctodæum. The partition walls between the three sections of the alimentary canal are subsequently absorbed.

The primitive band becomes more marked as development progresses, extends forwards at the lateral margins of the orifice of the stomodæum, and expands in front of this orifice into a pair of broad lobes, which form the sides of the head—the procephalic lobes.

The primitive band is now seen to be divided by fine transverse lines into a number of metameres or somites. This division commences immediately behind the stomodæum. Three somites are first formed; others succeed behind these until the whole length of the primitive band is segmented. Two lateral buds now appear, one on each side, on several of the anterior somites, commencing on the somite immediately behind the mouth, and appearing in order from before backwards. These are the rudiments of the ventral appendages—the jaws and legs. It will be observed that there is no segmentation of the parts in front of the stomodæum, the procephalic lobes and their pedicles. As in vertebrates, all the primitive somites are post-oral.

The appendages of the first three somites always become the mouth-organs, and form a pair of mandibles, a pair of maxillæ, and a labium or lower lip, which is formed by the more or less complete union of the third pair of lateral appendages.

The nature of the labium is very manifest in the Orthoptera, Coleoptera, and Hymenoptera, even in the perfect insect.

The three succeeding pairs of ventral appendages become the thoracic limbs (legs). The number of post-oral metameres which enter into the composition of the head is invariably three, and the same number belong to the thorax; all the remainder are abdominal. There are probably rarely less than nine, or more than eleven, of these in the embryo. The

greater number is characteristic of the Orthoptera. In the Diptera there are nine abdominal somites in the embryo, although the number of obvious segments in the perfect insect is usually greatly reduced.

A pair of nerve ganglia are developed from the cells which form the inner surface of each post-oral somite. These ganglia are united by a pair of nerve cords, longitudinal commissures, and also by transverse commissures between the ganglia of each pair.

In all the higher Insecta, and more especially in the true flies, there is subsequently a great concentration of these ganglia, which lose their relations with the somites in which they are first formed and become united into a single complex centre.

The longitudinal commissures are continued round the stomodæum and terminate in the cephalic nerve-centre, the brain, which is developed from the cells forming the inner surface of the procephalic lobes, and consists therefore of two symmetrical halves. Hitherto great discrepancies have existed in the works of comparative anatomists with regard to the number of somites which take part in the formation of the head. This arises from the attempt to regard the whole head as segmented. Thus some speak of five, and others of six, or even seven, cephalic segments, making two, three, or four of these pre-oral, and homologising the great eyes, the antennæ, and even the upper lip and the ocelli, with the thoracic and stomal limbs (mandibles and maxillæ).

Development lends no probability to such views, as there is no segmentation of the pre-oral region. It is true the antennæ present some similarity to the ventral appendages, and the stalked eyes of the higher Crustacea give an appearance of truth to the hypothesis that the eyes and antennæ are modified limbs. As both are developed from the procephalic lobes, and the latter at least do not at any period present the faintest resemblance in position or mode of origin to the ventral appendages, I am unable to see any reason for regarding either as homologous with the post-oral appendages.

The lateral and dorsal regions of the embryo are ultimately enclosed by the extension of the edges of the primitive band over the whole yolk, thus forming a somatopleure, or body-wall.

The embryo is usually, perhaps always, provided with an amnion (Fig. 2, *a*, *a'*), developed like the amnion of vertebrates

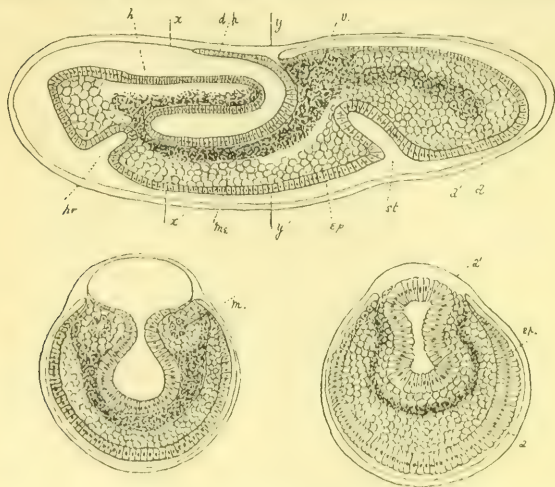


FIG. 2.—A longitudinal and two transverse sections of the embryo in the egg eight hours after impregnation. The plane of the left-hand lower figure is indicated by the line *xx'*, and of the right-hand figure by *yy'* in the longitudinal section; *a'*, outer layer, *a*, inner layer, of the amnion; *ep*, epiblast; *st*, stomodæum; *me*, mesoblast; *h*, hypoblast; *pr*, proctodæum; *v*, vitelline spherules; *d. p.*, dorsal plate covering the blastopore; *m*, Malpighian vessel. All these figures are drawn from actual sections.

from the epiblast, and commencing as a reduplication of the margin of the somatopleure of the embryo. It also connects the somatopleure with that portion of the blastoderm which covers the dorsal surface of the yolk behind the blastopore.

So far, the account I have given of the development of the

embryo differs in no material points from that given by the late Professor Balfour in his comparative embryology; except in relation to the origin of the alimentary canal, in which my observations agree with those of Bütschli. My own investigations, however, enable me to add the following important statements, which will be more fully discussed in another chapter:

The primitive hypoblast behind is, I believe, the dorsal plate of Kowalevski.\* It becomes concave above, forming a semi-cylindrical groove, the edges of which ultimately unite from before backwards. The cavity so enclosed remains continuous with that of the archenteron, and forms that portion of the intestine between the vessels of Malpighi and the rectum, which is usually regarded as originating from the proctodæum. It is perhaps a part of the mesenteron, but for the sake of clearness I shall term it the metenteron.

The metenteron is ultimately enclosed by the upward growth of the somatopleure, the edges of which meet and unite above it.

The dorsal vessel appears between the somatopleure and the metenteron; and the Malpighian vessels are developed as hollow processes of the hypoblast at the junction of the mesenteron and the metenteron.

The relations of the blastoderm to the yolk are somewhat different in birds and in insects, so far as the *Diptera* are concerned at least. If all the food-yolk of the bird's-egg were transferred from the under surface of the hypoblast to the cavity between the hypoblast and epiblast, or primitive cœlom, the hypoblast would correspond to the dorsal plate of the insect's egg, and the amnion of the bird would have the same relation to the epiblast and hypoblast as that of the insect.†

**Ecdysis.**—In all insects, as in arthropods generally, growth

\* Kowalevski, A., 'Embryologische Studien an Würmen und Arthropoden.' Mem. Acad. Sci., St. Petersburg, Bd. xvi., 1871.

† These views were first promulgated by me in my Hunterian lectures, February, 1890.

is attended by periodic sheddings of the cuticular layers of the skin, which are known as ecdyses, or moults.

Before each ecdysis the hypodermis separates from the cuticle, and a new cuticle is formed beneath the old one. The new cuticle remains soft and extensile for some time after the old cuticle is shed, and so permits of a considerable increase of size. This is effected generally in insects by the expansion of the air-vessels. The new cuticle then becomes hard and inextensile, checking all further increase in size until the next ecdysis.

Not only the external cuticle, but the cuticular lining of the alimentary canal and of the tracheæ, is shed at each ecdysis.

**Metamorphosis.**—These periodic ecdyses are sometimes attended by great and apparently sudden changes of external form, habits, and structure, known as metamorphoses; thus three stages are commonly recognised in the life-history of an insect: the larva, the pupa or nymph, and the imago or perfect form.

**The Larva.**—Amongst the spring-tails (*Thysanura*), the curious genera *Campodea* and *Sapyx* closely resemble the newly-hatched larvæ of many insects of widely different orders; such hexapod larvæ are spoken of as exhibiting the campodea form. The May-fly (*Cloëon diptera*) is developed from such a larva by a series of many moults, without any marked change of form before the last moult. The Earwig (*Forficula*) is developed in the same manner, but more rapidly with fewer moults; and the Rove-beetles (*Staphylinidæ*) have a campodea larva, but pass through a nymph stage before they attain sexual maturity.

Certain Coleoptera, *Sitaris*, *Meloe* and its allies, the genus *Mantispa* amongst the Orthoptera, and probably many other insects (Brauer\*), are hatched as active campodea larvæ, but soon lose their legs and become grubs, probably at the first moult. This phenomenon was called hypermetamorphosis by Faivre. The grubs are parasites on other insects, and after attaining their full size become nymphs.

\* Brauer, F., 'Beschreibung der Verwandlungsgeschichte der *Mantispa Styriaca* und über die sogenannte Hypermetamorphose Faivre's.' Verh. Zool.-Bot. Gesellsch., Wien, Bd. xix., 1869.

Many larvæ are, however, vermiform when they leave the egg, and either possess or are without rudimentary legs. Such larvæ are characteristic of the highest forms of insect life, and always pass through a nymph stage, in which there are usually no active manifestations of vitality.

Putting all these facts together, it is evident that the vermiform, or caterpillar form, of the larva is an acquired one. Those insects which exhibit the least differentiation of structure resemble a campodea larva even in their sexually mature condition, and are gradually developed from larvæ like themselves, so that there is ecdysis, but not metamorphosis.

Where wings are developed in the last stages, they are acquired gradually, becoming larger at each moult. Such insects have been classed as *Ametabola*. The development in these insects takes place chiefly in the egg, and the eggs are always comparatively large in proportion to the adult insect, and comparatively few in number. This is especially the case where the perfect insect exhibits special peculiarities, as, for example amongst the grasshoppers and *Phasmidæ*, and the larva is produced from the egg, not as a non-differentiated campodea larva, but having the general characters of the perfect insect.

Those insects which are most specialized, or, in other words, most highly organised, do not exhibit the campodea stage, but the larva is already vermiform when it leaves the egg. Development in the egg is arrested at an early period, as in the fly, and does not recommence until the larva has attained its full growth. Harvey had an intuition of this; he says: 'The eggs of insects do not contain a sufficiency of nourishment for the production of the young, which is born as a larva, and, after feeding and collecting a sufficiency of nutriment, returns to the condition of an egg in the pupa, from which the perfect insect is developed.' Such insects produce comparatively small, but usually very numerous, eggs, and are known as *Metabola*. The larvæ are chiefly characterised by the great activity of the organs of vegetative growth, and by the compara-

tively rudimentary condition of those which are needful for the protection and dispersion of the individual.\*

**The Resting Larva.**—Before each ecdysis the larva ceases to feed, generally seeks a place of safety, and becomes languid and motionless. The duration of the period which elapses before it again commences active life is greater the more profound the changes which occur at the moult. This phenomenon is especially marked before the formation of the nymph in the Metabola; some caterpillars remain inactive for months before they moult and reveal the contained nymph, which is developed during the resting period. In the Diptera and Hymenoptera the larva skin frequently becomes modified and replaces the silk cocoon which many larvæ spin for the protection of the nymph.

**The Pupa and Nymph.**—The general use of these terms is misleading. A pupa has been defined as a resting nymph, a nymph as an active nymph. If they were used in agreement with this definition no further objection could be made than that the term pupa is unnecessary, but the resting nymph of a lepidopterous insect is not the same thing as the pupa of a fly. The pupa of the fly is a resting larva, and the nymph, which is similar to the resting nymph of a butterfly, is developed within it. I shall, therefore, use the term 'pupa' for the final stage of the resting larva (*pupa coarclata*), and shall always use the term 'nymph' for the so-called *pupa oblecta*, which is the imperfect imago.

In insects with an incomplete metamorphosis, the manner in which the wings are developed is very instructive, and forms a key to the manner in which the nymph is formed in the higher, or more specialised, forms of insects.

Previously to the ecdysis, when the rudimentary wings become external organs, the hypodermis separates from the cuticular layer of the integument in the region where the rudimentary wing appears, and the wing is formed as an outgrowth from the surface of the separated hypoderm beneath

\* See also Brauer, F., 'Ueber die Verwandlung der Insecten.' Verh. Zool.-Bot. Gesellsch., Wien, Bd. xix.

the cuticle; the wings are similarly developed in caterpillars.\*

In the hairy caterpillars of the Lepidoptera, as De Reaumur showed, the hairs on the new integument are formed in the same way, and not in the interior of those which clothe the integument which is about to be shed.

In the hymenopterous vermiform larva, according to Dewitz,† the first rudiments of the legs of the imago are similarly formed in the young larva, but before the ecdysis they sink, as it were, beneath the hypoderm, which forms flask-shaped involutions around them, so that they are not revealed at the next ecdysis, but remain as embryonic rudiments until the larva attains its full growth, and only appear externally at its last ecdysis, when it passes into the nymph stage. In general all the structures which are peculiar to the imago in the Metabola are produced from such encapsulated rudiments, which are known as imaginal discs.

**Imaginal Discs** (Fig. 3).—This term was first applied by Weismann to certain encapsulated groups of embryonal cells closely related to the central nervous system in the larvæ and young pupæ of certain Diptera. They differ in no way materially from the rudiments of the legs of the hymenopterous nymph which appear in the larva, except that they arise in the embryo or very young larva, and during the growth of the latter they remain closely attached to the nerves and tracheæ, and apparently lose all connection with the hypodermis. This is, however, only apparently the case, as later observers have repeatedly detected the long drawn-out neck of the capsule of hypodermis in which they are enclosed, passing into the subcuticular hypodermis of the part from which they originate. Indeed, Weismann saw these bands, but did not correctly interpret them. No doubt, however, can exist any longer on this point, as will be sufficiently demonstrated in the course of this work.

\* E. Verson, 'La formazione delle ali nella Larva del Bombyx mori.' R. Stazione Bacologica sperimentale Pubblicazioni dal Ministero di Agricolt. ind. E. Comm. With two plates. Padova, 1890.

† Dewitz, 'Beiträge zur Kenntniss der Postembryonalen Entwicklung der Gliedmassen bei den Insecten.' Zeitsch. f. w. Zool., Bd. xxx., suppl. 1878.

Weismann supposed that only the integument (hypoderm) of the nymph is developed from the discs, but it is now certain that they consist of both epiblast and mesoblast, and that all the tissues of the nymph are re-developed from these and similar rudiments.

**Nomenclature of the Embryonic Rudiments of the Nymph.**—The term 'imaginal disc,' although very appropriate for the structures from which the head, thorax, and abdomen, with their appendages, are developed, is less suited for the designation of the rudiments of the viscera and nervous system. Künckel d'Herculais\* proposed to substitute the term 'histoblast,' but this met with no general acceptance; it may, however, be useful as a general term for those rudiments which are destined

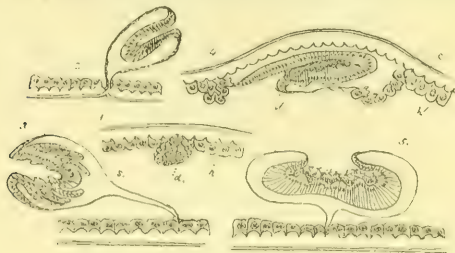


FIG. 3.—A Semi-diagrammatic Representation of the Imaginal Discs. 1, a simple disc; 2 and 3, leg discs; 4 and 5, wing discs; c, cuticular layer of skin; h, hypoderm cells; s, sac of disc; d, disc.

to form the viscera (splanchnoblasts) and nervous system (the neuroblast).

**Histolysis.**—It will be seen that there is no marked line of demarcation between the Ametabola and the highest Metabola, so far as the origin of the organs of the imago is concerned; but the two groups are distinguished by other phenomena—those of histolysis, or the degeneration of the larval tissue—of the highest significance, which separate the most specialised Insecta, with a rapid metamorphosis, from the less specialised,

\* 'Recherches sur l'Organisation et le Développement des Volucelles.' Fol., Paris, 1875-81.

in which the developmental changes of the internal organs at least present a more usual character.

In the most specialised Metabola all the larval organs and tissues are rapidly broken up, and converted into a cream-like pseudo-yolk, which serves as a pabulum, or food-material, for the development of the nymph and imago.

The nymph is practically a new embryo formed entirely from the imaginal discs and histoblasts of the larva, and the imago may be regarded as the fully-developed nymph after it has undergone a final or, in rare cases, a penultimate ecdysis.

In many of the Metabola the process of histolysis and regeneration occur simultaneously, and the nymph is already considerably developed before any of the larval tissues are entirely broken up, but in the Diptera (Muscidæ) it sometimes happens that all the larval tissues are converted into a granular pseudo-yolk before the nymph is formed, so that on opening the pupa it is found to contain an ovoid capsule filled with pseudo-yolk, in which the imaginal discs still remain un-united with each other. This stage I shall designate the pro-nymph. De Reaumur was the first to observe that a distinct stage occurs in the development of the Muscidæ not found in the other Metabola. He wrote: 'The worms which become flies with two wings make a shell of their own skin and pass through an extra metamorphosis, which caterpillars do not exhibit, that of an elongated ellipsoid, before they become nymphs' [1, tom. iv., pp. 296, 297].

**Relation of Metamorphosis to Ecdysis.**—Dr. Weismann, writing in 1864, said: 'In recent times it is well known that the change from the larva to the pupa state has been regarded as a moult, differing only in degree. But in the pupa formation of the Muscidæ the nature of the change precludes this view' [2, p. 162]. More recent observations nevertheless tend to show, I think very distinctly, that ecdysis and metamorphosis differ in degree rather than in their essential character. The researches of Barrois show that a perfectly parallel series of phenomena occur in the development of the Nemertid worms. Discs are formed as invaginations of the epiblast, which by

their subsequent union form the perfect worm, the remainder of the epiblast being detached and shed. Moreover, similar phenomena occur amongst echinoderms, a fact recognised distinctly by Dr. Weismann, who compared the metamorphoses of the Diptera with those of the Echinodermata, which at that time were regarded as a form of alternate generation (metagenesis), a view strongly, and I think successfully, combated by Barrois.\*

Nevertheless the change from the larva to the nymph in the flies is so complete that not one single organ is common to the larva and the imago. In the words of Harvey,† there is a complete return to the egg and a re-development of the insect. Taken as an isolated phenomenon, the development of the nymph in these insects might be regarded as an alternation of generation; but viewed in the light of comparative morphology, it appears only as an extreme case of metamorphosis, connected, by a long series of transitional phenomena, with simple ecdysis, accompanied by a gradual change of external form and internal structure.

\* Barrois, 'L'Embryologie des Nemertes,' Ann. Sci. Nat., ser. iii., tom. vi., 1877.

† Harvey, Gulielmi, opera omnia a Coll. Med. Lond., edita 1766, 'De Generatione Animalium,' ex. ii., p. 183.

### CHAPTER III.

#### ON THE GENERAL CHARACTERS OF THE ORDER DIPTERA AND ITS SUBDIVISIONS, WITH A DESCRIPTION OF THE TYPE FORM, '*CALLIPHORA ERYTHROCEPHALA*.'

THE blow-flies belong to the family *Muscidæ*, one of the most highly specialised groups of the Diptera, the most highly specialised order of the class Insecta. The Diptera are distinguished from other insects by the reduction of the wings to a single pair, which are situated on the meso-thorax; the posterior or meta-thoracic wings are present in a remarkably modified condition, as halteres, or balancers, and have a very complex sensory organ in their base, which is perhaps concerned in audition, so that the halteres cannot be regarded as

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#### Bibliography.—

11. SCHINER, J. R., '*Die Fliegen-Fauna Austriaca*.' Wien, 1861.
12. BRAUER, F., '*Monographie der Cæstriden*,' mit 10 Kupfertafeln. Herausgegeben von der K.-K. Zool.-Bot. Gesellsch. in Wien. 1863.
13. BRAUER, F., '*Kurze Charakteristik der Dipteren-larven*.' Verhand. der Zool.-Bot. Gesellsch. in Wien. Bd. xix., 1869.
14. BRAUER, F., '*Die Zweiflügler des Kaiserlichen Museum zu Wien*.' Part III. '*Systematische Studien der Dipteren Larven*.' Denksch. der K. Akad. der Wissenschaft. Mathemat. Naturwissensch. Classe. Bd. xlvii., 1883.  
Contains a complete bibliography of descriptions of dipterous larvæ. Parts I. and II. of this paper are systematic and on various genera and species. Part I., *ibid.*, Bd. xlii. 1880. Part II., *ibid.*, Bd. xliv. 1882.
15. OSTEN-SACKEN, C. R., on Mr. Portchinski's publications on the larvæ of *Muscidæ*. Berlin. Ent. Zeitsch. Bd. xxxi., pp. 17-27.  
An abstract in English of his comparative biology of necrophagous and coprophagous larvæ.

rudimentary wings, but are wings which have become subservient to a new function, and have undergone a corresponding modification of structure. The mouth organs in the Diptera are also so different from those of other insects that they have been the subject of much controversy, and their morphology has never been satisfactorily settled; the parts of the mouth are exceedingly complex, and differ far more profoundly from the primitive type than either the tongue of the bee or the spiral antlia of the Lepidoptera.

Haeckel regarded the Coleoptera, or beetles; the Hymenoptera, or bees and wasps; the Lepidoptera, butterflies and moths; and the Diptera, or two-winged flies, as the extreme modification of four separate and divergent genetic series, just as mammals, birds, and reptiles are amongst the vertebrates. The Coleoptera have apparently descended from Orthoptera; the Hymenoptera and Lepidoptera from Neuroptera; and the Diptera from Hemiptera: or rather from ancestral forms similar to those which form these less specialised orders. Just as all discussion would be futile as to whether a bird or a mammal is the higher type, so it is useless to consider whether the Diptera or the Hymenoptera have the higher organisation; but there can be no question as to which of these orders departs most from the more generalised form. The Diptera are far more remarkable in their developmental history, and in the modification of structure which they present in the adult or imago form. In this relation the strong tendency of many to produce their young alive, and the fact that some have a capacious matrix, or uterus, in which the larvæ are hatched, or even attain the pupa form, before birth, is not without interest—presenting as it does some analogy with the viviparous character of the Mammalia amongst vertebrates—whilst the nest-building instincts are more manifest in Hymenoptera and in birds. It is true that the flies, and more especially the heavy forms, with a comparatively tardy flight, like the blow-fly, have been regarded as ‘stupid’—Sprengel called them ‘die dumme Fliegen’—and do not excite our sympathy and curiosity to the same extent as the social Hymenoptera; but

it is impossible to judge of the intellectual functions of an insect. The manner in which the blow-flies and their near allies, the house-flies, have made themselves at home with man speaks for their power of adapting themselves to new and varied conditions. They are cunning, wary and easily alarmed, and, except when benumbed with cold or heavy with eggs, know well how to avoid danger. They appear to me far more clever in this respect than the bees or wasps.

The Diptera are specifically and numerically the most abundant of all insects, and exhibit a wide range in organisation, so that we may arrange them in lower and higher groups, or, to use the language of the evolutionist, we may regard the order as consisting of ancient and modern forms. The members of the lower subdivision of the order retain a larval condition similar to that of the Hymenoptera, Coleoptera, and Lepidoptera in their most differentiated form, and undergo a gradual metamorphosis. The larval skin splits along the back for the escape of the nymph, and some spin a silken cocoon for its protection: such Diptera are said to be orthoraphic.

The higher Diptera have a larva which is apparently headless; they form a pupa, the external covering of which is the modified larval skin, which splits by a circular fissure, for the escape of the imago: such Diptera are said to be cycloraphic. In these the nymph is developed rapidly within the larva after the complete histolysis of all its tissues, so that the perfect insect is more nearly related to the embryo than to the larva, and the nervous system of both larva and imago is highly concentrated and exhibits great complexity.

**The Larvæ of the Diptera.**—Dr. J. R. Schiner [11] gives the following description of the dipterous larva. He says: ‘They have as a rule an annulate form, and may be divided into two easily distinguished groups: those which have a distinct chitinous head capsule, *eucephalæ*; and those in which the head is scarcely distinguishable, *acephalæ*. The latter, which are designated “headless,” are devoid of eyes, antennæ, and feet. This form of larva is known as a maggot. The dipterous larvæ have usually thirteen segments, of which the head is the

first. The second, third, and fourth form the thorax, and the remainder belong to the abdomen. The relative length and thickness of the abdomen varies much in different species. The skin is, as a rule, very soft, and is usually whitish, although it is sometimes thick and almost leatherlike, and is occasionally intensely coloured.

‘The mouth armature of the headless larvæ is very simple, and consists of two black pointed hooks near the anterior part of the head. That of the eucephalic larvæ can be distinguished in certain species as consisting of an upper and under lip, mandibles, maxillæ, and even maxillary palpi, as in the larvæ of the Coleoptera. In the eucephalæ simple eyes, antennæ or their rudiments, and false feet are usually present. The latter are conical truncated organs provided with hairs or hooks, situated on the ventral surface of the annuli of the body, and used in some species as organs of progression. The larvæ of a few spring by the elongation and rapid contraction of the body.

‘In some the stigmata or breathing pores are found on the middle rings, *peripneustic larvæ*; in others they only occur on the first and last segments, *amphipneustic larvæ*, or are confined to the last segment, *metapneustic larvæ*.’

They are either terrestrial or aquatic, and exhibit very great variations of form. Many eucephalic larvæ have a pair of false feet on the first thoracic segment, and these and the abdominal false feet may be provided with spiny cushions or suckers. The nervous system consists of thirteen ganglia, two cephalic, three thoracic, and eight abdominal, but sometimes these are concentrated into two nerve-centres (Brauer).

Brauer says, ‘The recognition of the mouth organs in the larva is very difficult, owing to the very unequal development of the head;’ he does not attempt to determine the comparative morphology of the hooks and tubercles which form the mouth armature of the acephalæ, but suggests that the great hooks of these are maxillæ (Unterkiefer?) [14, p. 33].

It has long been known that the head-capsule amongst many of the eucephalæ is very rudimentary, and Hammond, I think, first demonstrated that this is due in the Crane-flies

to the invagination of the head-capsule within the thorax. The invaginated portion of the head-capsule is deeply cleft both on its dorsal and ventral surface. In other Nematocera and many Tabanidæ this condition is still more marked, and the head-capsule is reduced to the form of diverging chitinous rods in relation with the pharynx (Fig. 9). These are termed 'Zopfgräten' by Brauer.\* I shall speak of such rods as the cephalo-pharyngeal apophyses; they apparently represent the inflections which form the endo-cranial skeleton in more perfectly developed head-capsules, and afford a key to the morphology of the so-called pharyngeal skeleton of the acephalous larvæ.

The division of the order into orthoraphic and cycloraphic sub-orders was first suggested by Brauer [12], and is undoubtedly morphologically correct; it has not, however, the advantage of being of ready application; first, because every variety of transition exists between the lowest orthoraphic and the highest cycloraphic forms; and, secondly, because in many cases the developmental history of a species is unknown. Hence systematic entomologists need a more artificial division founded upon characters which are externally manifest in the imago. The Diptera are therefore generally divided into the four following sub-orders: Aphaniptera, Nematocera, Brachycera, and Pupipara.

These sub-orders are not, however, of equal import. The Nematocera are a fairly natural group, but the Brachycera consist of at least two distinct sub-divisions of the Diptera. The Aphaniptera are nearly related to the Nematocera, and are a semi-parasitic and probably degraded group, formerly classed with the Hemiptera. The Pupipara, on the other hand, are related to the higher forms of Brachycera, but are also parasitic insects, exhibiting very remarkable modifications both in their development and structure.

**The Aphaniptera**, or fleas, although almost apterous, having only scale-like rudiments of wings, present so many points of affinity with the Diptera that they are included in the order by most modern systematists.

\* Consult Brauer's [14] figures of the head of *Limnophila*, *Pæcilstola*, *Dolichopus*, *Tabanus*, etc.

The **Nematocera** are very numerous, and are distinguished by their long-jointed antennæ, which are sometimes plumose in the males. They are all orthoraphic, and often have larvæ with a well-developed head-capsule, sometimes invaginated within the thoracic segments (*Tipula*). They frequently exhibit a transition between insects with a complete and an incomplete metamorphosis, and have active nymphs; the larva and nymph are also often aquatic. The former, in the gnats, has a resemblance to the Zoea stage of the Crustacea, and Fritz Müller and Hæckel have suggested this as a probable early ancestral form of the Insecta (Brauer).\* The best-known genera are *Cecidomyia*, *Chironomus*, *Corethra*, *Tanypus*, *Culex* and *Tipula*.

The **Brachycera** are divided into *Tanystomata* and *Muscaria* by some, but the sub-order presents exceptional difficulties; perhaps the *Tanystomata* should be further subdivided.

The **Brachycera** are all distinguished by having short antennæ, consisting of three joints; the third or terminal joint is largely dilated and contains the olfactory organ.

The **Tanystomata** all have a more or less developed head-capsule in the larva, and have orthoraphic pupæ or naked nymphs, which escape from the larval integument by a longitudinal dorsal fissure. The best-known forms are *Tabanus*, *Asilius*, *Bombylius*, *Empis* and *Dolichopus*.

The *Tabanidae*, *Asilidae* and other orthoraphic *Brachycera*, when they arrive at their final stage of development, closely resemble the cycloraphic *Diptera*, but their larvæ exhibit a transitional condition between the eucephalic nematocerous larva and the highly modified acephalic larva of the *Cycloraphia*.

The **Muscaria** are the most highly modified *Diptera*; their larvæ have an incomplete head and a rudimentary internal head-capsule. They are all cycloraphic, and are divided into *Acalypterata* and *Calypterata*. The former have no wing-scales, and the latter, to which the blow-fly belongs, have large wing-scales which cover the halteres.

The **Pupiparæ** are only separated from the *Brachyceræ* by the remarkable character of their metamorphosis. The young are developed singly within the uterus of the mother, which deposits young pupæ instead of eggs; thus there is no true larva stage, but a gigantic embryo is transformed directly into a pupa. They are all parasitic, and are the *Nycteribiæ*, *Hypoboscidae*, and *Braulidae*. The two first are parasitic on birds and mammals, and the last on bees.

The genera of the *Muscidae* are exceedingly numerous, and include about one third of the *Diptera*; many differ by small, and apparently unimportant, details.

**Musca.**—The old genus *Musca* has been divided and subdivided. Now it is much restricted by the formation of new genera; so that in the latest catalogue of British *Diptera*† it includes only two species, the house-fly (*Musca domestica*) and the small house-fly (*M. corvina*). The flesh-flies (*Sarcophaga*) form a distinct family, and the blow-flies constitute the three subgenera, *Lucilia*, *Calliphora*, and *Pollenia*.

\* Verh. Zool.-Bot. Gesellsch., Wien, Bd. xix., p. 301.

† 'A List of British *Diptera*,' by G. H. Verrall, small 4to, London, 1888.

The characters of *Musca* are defined in the following manner :

Cycloraphic calypterate Brachycera, with a soft, fleshy proboscis without lancets, developed from a larva with a single pair of anal feet, a rudimentary head provided with two strong hooks, and with two pairs of spiracles, one pair in front and the other near the posterior end of the body. The adult insect has a long bristle on the third joint of the antenna fringed with short hairs on both sides quite to its tip. The three subgenera, *Lucilia*, *Calliphora*, and *Pollenia*, are distinguished from *Musca*, as defined above, by very trivial characters.

The following description will serve to identify *Calliphora erythrocephala*:

***Calliphora erythrocephala*** is the commonest British species ; it measures 6 to 12 mm. ( $\frac{1}{4}$  to  $\frac{1}{2}$  inch) in length, and 20 to 30 mm. from tip to tip of the extended wings. Head, black, except the semicircular space between the proboscis and the antennæ, which is brown or black, and the genæ, which are fulvous or golden-yellow ; beard, black. The back of the head and sides of the forehead often have a silvery pubescence.

Thorax, blue-black, with white pubescence above on each side. Wings, diaphanous and smoky, with black nervures ; nervures near the thorax, testaceous ; legs black.

The wings and the tarsi in some lights always have a rufescent pubescence, which in specimens from Eastern Europe is very well marked, and extends over the back of the thorax. The abdomen is of a deep metallic-blue, the anterior three-fourths of each segment being covered with white pubescence.

Sometimes both thorax and abdomen are violet with a greenish sheen ; possibly such insects are hybrids between *C. erythrocephala* and the allied *C. cognata*.

*C. erythrocephala* is sufficiently distinguished from all other *Calliphoras* and *Lucilias* by its fulvous genæ, black beard and blue-black abdomen. Some of the numerous allied genera might be mistaken for *Calliphora*, but differ in the nervures of the wing.

***Calliphora vomitoria*** is rare in England, and has a red beard and black checks ; in most anatomical works it is confounded with *C. erythrocephala*. The genus *Lucilia* is distinguished by the blue-green metallic lustre of the abdomen in these insects.

According to Portchinski [15], who investigated the larvæ of many species of Muscidae in both North and South Russia, the larvæ of *Lucilia caesar* and *Cynomyia mortuorum* are all exclusively carrion feeders and live entirely upon flesh, whilst those of *Musca domestica* and *Musca corvina* are coprophagous. The above-mentioned carnivorous larvæ are all so much alike that Portchinski was unable to find any difference in them.

*Musca corvina* differs from all the rest in the large size of its eggs. This insect lays only twenty-four eggs, and the larva only exhibits two instead of three stages in the development of the spiracles.

*Musca corvina* is exceedingly abundant in the Crimea and the Caucasus. Early in spring these flies are oviparous, but in the late spring and summer they are viviparous, and deposit larvæ in the third stage of development.

Portchinski ventures on the hypothesis that the Pupiparæ were originally coprophagous insects in the larva state, and laid an almost full-grown larva, like *Musca corvina*.

## CHAPTER IV.

### THE LARVA OF THE BLOW-FLY.

#### 1. EXTERNAL FORM AND SEGMENTATION.

**External Form.**—The larva of the blow-fly is well known as the gentle or maggot. It is a soft-skinned, cylindrical, wedge-shaped worm, gradually increasing in diameter from before backwards, and truncated behind obliquely, so that the posterior extremity exhibits a concave surface, which looks upwards and backwards, within which the great posterior spiracles are situated.

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**Bibliography.**—Papers on and references to the larvæ of various Dipterous insects are very numerous, but those which treat on their anatomy are few, and usually short. The majority are descriptions of external form and habit.

BRAUER [14] gives 47 quarto pages of bibliography, arranged under genera and species. The *Cestrinæ*, the larvæ of which differ little from those of the *Muscidæ*, have been chiefly studied; and Brauer, in his monograph on the family, gives a full bibliography to 1861.

Special references to papers on several organs are given under the sections of this chapter.

16. BOUCHÉ, 'Beiträge zur Insectenkunde.' 1. Bemerkungen über die Larven der Zweiflügligen Insecten. *Nova Acta. L. C. Acad.* Bd. xvii., p. 495. (1833) 1835.
17. SCHRÖDER, VAN DER KOLK, 'Mémoire sur l'Anatomie et la Physiologie du *Gastus equi*,' avec 13 pls. *Verhand. d. Kl. Nederl. Inst.*, D. ii., p. 1-155. 1845.
18. DUFOUR, LÉON, 'Études Anatomiques et Physiologiques sur les Insectes Diptères de la famille des Pupipares.' *Ann. Sc. Nat. Zool.*, ser. iii., tom. iii., 1845.
19. DUFOUR, LÉON, 'Recherches Anatomiques et Physiologiques sur les

**Segments.**—The integument is obviously divided by circular sulci into a series of rings or segments. If the small head be considered the first segment, the second, third, and fourth obvious segments belong to the thorax, and the second bears a pair of pedunculated spiracles. There are no spiracles on the segments which intervene between this and the last, so that this larva is *amphipneustic* (see page 28). Each segment has a thickened anterior border, covered by short recurved spines and sensory papillæ. The spines apparently prevent a retrograde movement in burrowing, like the setæ of an earth worm.

The abdominal segments exhibit a dorsal and a ventral arch, separated by a marked lateral fold, and the ventral arch is divided by a transverse sulcus into an anterior and posterior portion.

Although it would appear at first sight perfectly easy to count these segments, authors are by no means agreed as to their number. Dr. Weismann [2] gives twelve, reckoning the

- 
- Diptères.' Mem. Pres. à l'Acad. des Sc. Math. et Phys., tom. xi., pp. 171-360. 11 pl., 1851.
20. LEUCKART, R., 'Fortpflanzung und Entwicklung der Pupiparen.' Abh. Nat. Gesellsch., Halle, Bd. iv., 1858.
  21. SCHEIBER, S. H., 'Vergleichende Anatomie und Physiologie der Östriden-Larven.' Sitzungbericht der K. Akad., Wien. Bd. xli., pp. 409-496, 1860; and Bd. xlv., pp. 7-68, 1862.
  22. LEUCKART, R., 'Die Larvenzustände der Musciden.' Archiv. f. Naturgesch. Jahrg. 27, 1861.
  23. MARNÓ, ERNST, 'Die Typen der Dipteren Larven.' Verhand. der Zool. Bot. Gesellsch. in Wien. Bd. xix., 1869.
  24. HAMMOND, A., 'The Anatomy of the Larva of the Crane-fly.' Sc. Gossip, vol. xi., pp. 10, 171, 201. 1875.
  25. KÜNCKEL D'HERCULAIS, JULES, 'Recherches sur l'Organisation et le Développement des Volucelles.' Fol., Paris, 1875-81.
  26. BATELLI, ANDREA, 'Contribuzione all' Anatomia ed Fisiologia della Larva dell' Eristalis tenax.' Bull. della Soc. Ent. Ital., 1879, pp. 77-120, with 5 plates.
  27. VIALLANES, H., 'Recherches sur l'Histologie des Insectes et sur les Phénomènes histolytique qui accompagnent le développement post-embryonnaire de ces animaux.' Ann. Sc. Nat. Zool., ser. vi., tom. xvi., pp. 1-348. 18 pls., 1882.

head as the first; Schiner [11], as we have seen, gives thirteen as the general number in the dipterous larva. Weismann apparently overlooked a very obvious segment, between the head and the first thoracic segment. This is usually invaginated within the first thoracic segment, so that it cannot be seen except when the larva is forcibly extended; but New-

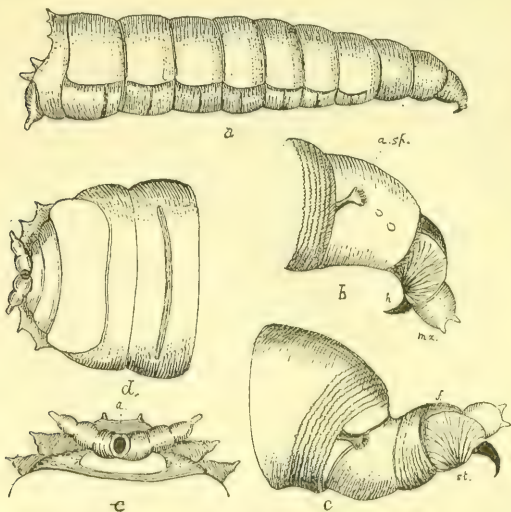


FIG. 4.—The Adult Larva of the Blow-Fly. *a*, lateral view; *b* and *c*, the head of the same in extension and flexion—*h*, the great hooks; *st*, the stomal disc; *mx*, the maxilla; *f*, the forehead; *a sp*, the anterior fan-like spiracle, with two lenticular bodies in front of it; *d*, the posterior extremity of the same; *e*, the last two segments, showing the anus (*a*) flanked by a pair of false feet. The sub-semicircular plate in front of the anus is the ventral plate of the anal (15th) segment.

port [9] correctly described it. I shall speak of it as Newport's segment. Brauer [14], like Weismann, gives twelve, but believes—and I think correctly—that the last segment is a complex of two.

Although it is convenient to speak of the head as the first segment, it represents the three first post-oral metameres of the embryo. I regard Newport's segment as the last of these cephalic metameres; the second is only represented by its ventral appendages, the maxillæ, which form the greater part of the head of this larva; and no traces of the first cephalic metamere can be distinguished externally, at least.

Adopting these views, the first thoracic segment is the fourth post-oral metamere, and is so numbered in my figures. The three cephalic, three thoracic, and nine abdominal segments, counting the last obvious segment as two, give fifteen post-oral somites, of which the first is apparently suppressed. And the second is only represented by its ventral appendages, the maxillæ. Formerly two pre-oral somites were added, making seventeen, a number which has usually been regarded as typical of all insects except the Orthoptera, which generally exhibit eleven abdominal segments.

The question as to the morphology of Newport's segment is one of considerable interest, and will be further discussed hereafter. The compound nature of the last segment is not, I think, doubtful, but is manifested by the existence of a pair of ventral appendages close to the anus, each consisting of three joints, with a small ventral plate in front of them (Fig. 4, *d* and *e*). The concave disc, which contains the posterior spiracles, is fringed with papillæ, of which four are large and eight smaller; five are situated on each side, and two below.

## 2. THE INTEGUMENT.

The *Integument* is thick and leather-like in the adult larva; its cuticular portion consists of two distinct parts: the *epiostracum* and the *endostracum*.

The *Epiostracum* forms a continuous layer over the whole external surface, and is inflected into the mouth, anus, and spiracles. It forms the solid recurved spines on the anterior portion of the segments, and the muscles are inserted into it

by means of fibres of a tendinous character, which run through the whole thickness of the endostracum (Fig. 1, *r*).

The **Endostracum** consists of many laminae, and is more or less distinctly divided into hexagonal columns, several corresponding to each of the cells of the hypoderm. It is perforated by numerous canals, which contain processes from these cells (Fig. 1, *r* and *s*) and nerve end-organs, which terminate in the sensory papillae (Fig. 1, *3*, *t*), immediately beneath the epiostracum.

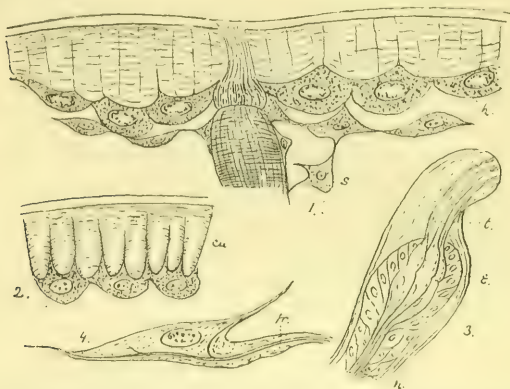


FIG. 1 (*bis*).—Sections of the skin of the Blow-fly larva.—1, a vertical section, showing the manner in which the muscles are inserted into the epiostracum; 2, a similar section, showing the prisms of the endostracum; 3, a sensory papilla; 4, a sub-hypodermic cell, with a terminal trachea in its interior. *cu*, Cuticle; *e*, end organ; *h*, hypoderm cells; *s*, sub-hypodermic cells; *t*, terminal portion of the end organ; *tr*, trachea.

**Sensory Papillæ.**—The surface of the integument, especially near the spiracles and on the anterior edges of the rings, is raised into papillæ, which consist of both epi- and endostracum. These papillæ contain bundles of fusiform cells, which terminate in very fine rod-like organs in the epiostracum at the tip of the papilla, these are the terminal organs of cutaneous nerves (Fig. 1, *3*, *t*).

**Lenticular Bodies** of a highly refractive character are found imbedded here and there in the endostracum, sometimes deeply, more usually immediately under the epiostracum. These bodies vary from .1 mm. ( $\frac{1}{10}$  of an inch) to mere granules. They are very hard and brittle and consist of concentric lamellæ enclosing an internal cavity. Several are found near the head. They apparently resemble the so-called calcareous bodies of cestoid worms (Fig. 4, *b*).

**The Hypoderm** consists of large flat hexagonal cells,  $70\mu$  to  $80\mu$  in diameter, and  $50\mu$  or more in thickness. The nuclei of these cells are distinctly vesicular,  $40\mu$  in diameter (see 'Histology'); some are cup-shaped next the cuticular layers, and the cavity is filled by the rounded inner extremity of the corresponding cuticular prism. Others are conical and fill cavities in the cuticle below the projecting papillæ on its surface. Many send fine processes through the canals of the endostracum (Fig. 1, *r* and *z*; *h*).

**Basement Membrane.**—Several authors have described a thin cuticular basement membrane beneath the hypoderm cells. Such a membrane only exists just before the formation of the pupa.

**Sub-hypodermal Cells** (Fig. 1, *r*, *s* and *z*).—Viallanes [27] first described a fenestrated layer of cells beneath the hypodermis, this is the connective tissue, or so-called peritoneal coat, which is reflected from the surface of the internal organs over the inner surface of the hypoderm; it supports the tracheal network. The individual cells are often stellate, and are continuous with the adenoid reticulum of the blood sinuses.

### 3. THE HEAD AND MOUTH ARMATURE.

**The Head.**—The only portions of the head which can be recognised externally are the maxillæ, separated on their ventral surface by the mouth, the prestomal and discal sclerites; and on their dorsal aspect by the epicranium.

**The Maxillæ.**—The organs which I have so named form by far the largest portion of the head, and each consists of two parts separated by a slight circular sulcus—a proximal and a

distal joint (Figs. 4 and 5). The distal portion is sub-hemispherical and has two short conical sensory papillæ at its extremity, one above the other; it contains a pair of sensory organs, which terminate in the papillæ. These closely resemble the eyes of a leech, except in being devoid of pigment; they are apparently sensitive to light (see Sensory organs).

The proximal portion is sub-cylindrical, and exhibits a very remarkable half-disc on its ventral and outer surface, the stomal disc (mihi), and in front of the stomal disc the orifice of a sac, in which the great hook lies when retracted.

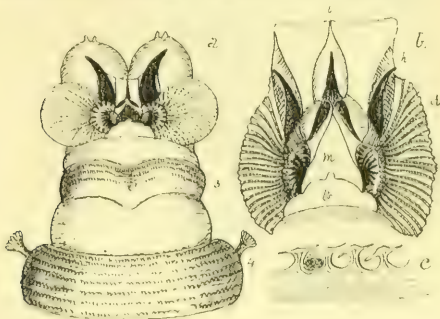


FIG. 5.—a, the head and mouth of the adult larva of the Blow-Fly seen from the ventral surface; 3, Newport's segment; 4, the prothoracic segment; b, the mouth more highly magnified ( $\frac{1}{2}$  inch objective); l, the prestomal sclerite; d, the stomal disc; m, aperture of the mouth; lb, the labium; c, transverse section of the pseudo-tracheæ of the stomal disc as seen with  $\frac{1}{2}$  oil immersion lens.

The real significance of these organs has been apparently overlooked by Weismann and most subsequent writers, except Macloskie\* and perhaps Brauer [14, p. 32], who recognised that the mouth parts of the larva correspond with the proboscis of the imago, without entering into details. This is more remarkable, as the development of the maxillæ is easily traced from the unmistakable maxillæ of the embryo, from which they scarcely differ, and these were correctly figured and described by Weismann, who, however, entirely neglected the correspond-

\* See page 44.

ing organs in the larva, and contented himself by describing the head in the following manner: 'The first and smallest segment exhibits the mouth opening on its ventral surface and two pairs of papillæ on its dorsal surface' [2, p. 105]; and although he subsequently describes the mouth organs at considerable length, he does not again refer to the maxillæ, except to mention 'two thread-like thickenings in the recently-hatched larva, which spring from the angle of the mouth and run

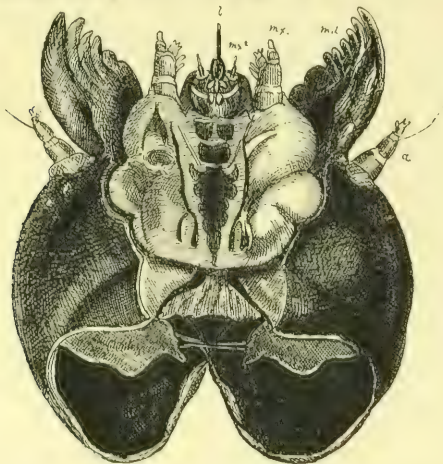


FIG. 6.—The head of the *Cossus* caterpillar after Lyonet. *a*, antenna; *md*, mandible; *mx*, maxilla; *mx<sup>2</sup>*, the second maxilla; *l*, ligula.

obliquely towards the back' [p. 108]; and adds, 'the two chitinous ridges of the newly-hatched larva are replaced in the adult by a fan-like group of similar ridges, which diverge from the angle of the mouth and form a half circle at the side of the mouth opening' [p. 109]. These are his only descriptions of the stomal disc. He refers subsequently to the two pairs of papillæ as the antennæ and maxillary palpi [p. 120].

A comparison of the maxillæ with those of a lepidopterous

larva (Fig. 6, *mx*) will assist the reader in attaining a clear idea of their relations.

The **Mouth** presents a triangular orifice between the proximal joints of the maxillæ; the apex of the triangle is in front and its base is formed by the labium.

The **Stomal Disc** exhibits a nearly semicircular surface, grooved by a number of radiating dichotomously-dividing channels, similar to the pseudo-tracheæ of the proboscis of the imago, but without ring-like thickenings (Fig. 5, *c*).

It is of considerable morphological interest, because the principal imaginal disc from which the proboscis of the fly is developed is formed by an invagination of its hypoderm.

The channels on its surface open into a cup-shaped cavity on the oral edge of the disc or by a single vessel, which is formed by the union of those of the posterior third of the disc, into the external angle of the mouth. These channels apparently serve to distribute the salivary secretion over the food and also to conduct the food into the mouth. They always contain a considerable quantity of grumous fatty material, and their contents are blackened intensely by osmic acid.

The **Great Hooks** are uncinatè processes of the cuticular layer of the integument, and when at rest are retracted within special cavities in the maxillæ (Fig. 8, *3, h*), which do not communicate with the mouth. They are the retractile claws of the maxillæ, and resemble the claws on the thoracic feet of some larvæ. In the recently hatched larva the great hooks are very small straight chitinous rods, the distal extremities of which are bent at right angles (Figs. 7 and 9), and like the claws on other feet are shed and renewed at each ecdysis. Before the second moult the new and old hooks are occasionally seen side by side, a fact recorded by Weismann.

Brauer [14, p. 33] calls these hooks maxillæ, but also speaks of them as mandibles, and does not assert their morphological identity with either; Menzbier\* supposed them to lie when retracted within the mouth, and regarded them as indurations of

\* Menzbier, M., 'Über das Kopfskelet und Mundwerkzeuge der Zweiflügler.' Bull. Soc. Imp. Nat., Moscow, t. 55, 1880.

its cuticular lining without morphological significance. In my former work\* I drew attention to the marked resemblance of these hooks to certain hook-like sclerites in front of the suctorial disc of the proboscis of the imago; I did not then know how closely this portion of the proboscis is connected with the great hooks of the larva in its developmental history.

These have only a secondary connection by articulation with the internal pharyngeal skeleton (Fig. 9, *3*) which supports them. They are used as organs of locomotion, and probably assist in the disintegration of the flesh in which the larva burrows.

Before entering upon any further description of the head of the larva, I shall explain the relation of its parts from a de-

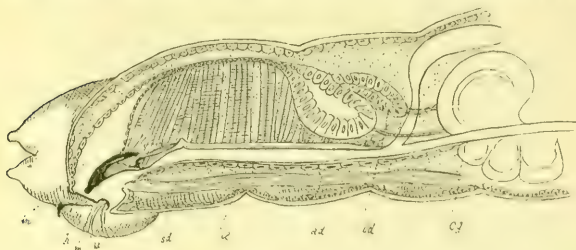


FIG. 7.—A vertical longitudinal median section through the anterior portion of a newly-hatched larva seen with  $\frac{1}{4}$  inch objective. The external portions of the head are added to the actual section—*in*, invagination of the forehead; *h*, lateral (great) hooks; *m*, median tooth (*labrum*); *st*, stomal disc; *sd*, salivary duct; *a*, œsophagus; *ad*, antennal disc; *od*, optic disc; *cg*, cephalic ganglia.

velopmental point of view. The retrogressive character of the final stages of development in the egg has already been alluded to (p. 2). A median section of the newly-hatched larva is given in Fig. 7. A strong median tooth *m*, is seen deeply imbedded between the maxillæ. This tooth is described by Weismann as the most important part of the mouth armature; it is not present after the first moult—and he regarded it as consisting of the united mandibles of the embryo.

\* 'Anatomy and Physiology of the Blow-fly.' London, 1870.

In front of and above this median tooth there is a remarkable invagination of the hypoderm (Fig. 7, *in*) which extends over the pharynx, and communicates with the sac from which the imaginal discs of the head of the nymph are subsequently developed. This invagination is undoubtedly the fore-head (Vorderkopf) of the embryo, which is invaginated between the maxillæ.

Below the median tooth is the true mouth orifice. The tooth itself is clearly the labrum, or upper lip; with which, I think it extremely probable, the mandibles are fused, although the evidence of this is obscure.

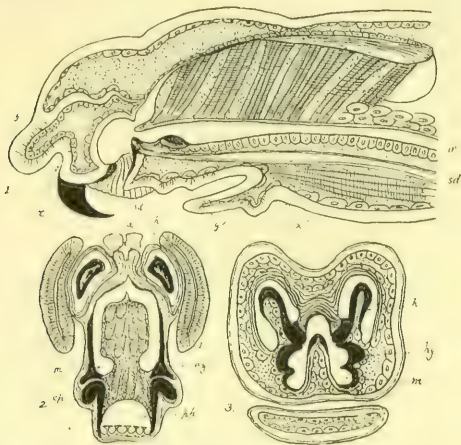


FIG. 8.—Sections of the head of the adult larva (40 diam.)—1, a vertical median section; *sd*, stomal disc; 2, a transverse section in the line *x x'* in 1. The curve is due to the position of the head, that represented in Fig. 4, *c*; *h*, the great hook; *hy*, hypostomal sclerite; *m*, mouth; *ph*, pharynx; *cp*, anterior inferior process of the cephalo-pharynx; *a*, œsophagus; *sd*, salivary duct. The section shows the grooves in the hypopharynx—3, section through the mouth and pharynx, in the line *y y'* in 1, showing imaginal discs 1.

Below and behind the labrum is the orifice of the salivary duct in the rudimentary ligula, which is undoubtedly the homologue of the ligula of the caterpillar, Figs. 6, 7 and 8.

In the newly-hatched larva the stomal discs are relatively

larger than in the adult, but each only exhibits a simple pair of channels, pseudo-tracheæ. When expanded the stomal disc of the young larva has a striking resemblance to the oral sucker of a trematode, and entirely surrounds the mouth.

**The Prestomal sclerite** (Figs. 5 *l* and 9 *2 pl*), is a ridge of chitin between the maxillæ; its posterior extremity in the newly-hatched larva forms a convex pad covered with minute bristles, and at this stage the discal sclerites (Fig 9, *2*) are slender rods diverging from the pad which support the pseudo-tracheæ of the disc.

In the adult larva (Fig. 5, *b*) these structures are more strongly chitinized, and are no longer connected with the pseudo-tracheæ; they form a kind of pseudo-labrum in front of the external larval mouth, but are not situated at the true orifice of the alimentary canal. Even in the adult larva the remains of the invaginated forehead are still distinctly recognisable in a median section between the prestomum and the anterior extremity of the pharyngeal apparatus, which corresponds with the median tooth, labrum, of the newly-hatched larva.

**The Labium**, or lower lip, remains external; it is broad from side to side, and narrow from before backwards (Fig. 5, *lb*). It exhibits a median and two lateral lobes, and almost covers the mouth orifice when the larva is not feeding; it is capable of being retracted by a pair of powerful muscles.

**The Pharynx**.—Immediately within the true or internal mouth orifice is the massive pharynx. Weismann describes it in the following terms: 'The pharynx is a cylindrical bulb, somewhat pointed in front and behind; behind it is continuous with the œsophagus, and it might be regarded as the thickened commencement of the œsophagus itself, were it not for strong morphological grounds, which compel us to take a different view. It originates in the embryo as an invagination of the forehead and mandibular segment' [2, p. 107]. This view of Weismann's is undoubtedly correct; but he advanced only slender evidence in its favour, so that subsequent writers have regarded the strong pharyngeal sclerites as chitinous thickenings of the alimentary tube.

The pharyngeal skeleton of the larva corresponds in all respects with the fulcrum of the imago. It consists of two vertical plates, connected above by a cross-bar (Fig. 9, *3*); these are the cephalo-pharyngeal apophyses. They enclose a cavity between them, which contains the intrinsic pharyngeal muscles, and are united below by the hypopharynx, a sclerite developed in the cuticular layer of the stomodæum or foregut. There is no distinct epi-pharyngeal sclerite in the larva.

The invaginated forehead lies above the stomodæal tube, and sends a hollow process downwards on each side of it. These processes correspond with the inflected edges of the clypeus in the imago. A sclerite is developed in the hollow of each of the processes; this is the lateral plate of the pharyngeal skeleton, which is therefore covered by hypoderm on both sides.

The connection between the involution of the edges of the clypeus and the imaginal discs is well seen in *Chironomus* (Hammond, *in lit.*).

The cephalo-pharyngeal apophyses of the eucephalic larvæ of the Diptera are, without doubt, the chitinized margins of the plates of the head capsule,

which are more or less inflections of their edges, and correspond closely with the internal cephalic skeleton of more perfectly developed head-capsules, such as that of the caterpillar (Fig. 9, *6*), from which the dilator muscles of the anterior portion of the alimentary tube arise.

These must all therefore be regarded as morphologically similar structures, which are represented in the imago of the Diptera by the so-called fulcrum, only a very small part of which, the hypopharynx, arises in the wall of the stomodæum.\*

The part of the dipterous mouth which has been identified with the hypopharynx by all recent writers is a totally distinct structure, which I term the ligula, and has no relation to the hypopharynx of Savigny, which is a plate developed in the lower wall of the stomodæum.

As the pharynx is therefore exceedingly complex, I shall speak of the whole organ, the skeletal structures and the muscles, as the fulcrum; that portion of the skeleton which belongs to the head-capsule I shall term the cephalo-pharyngeal skeleton, or, for brevity, the cephalo-pharynx; that portion developed in the wall of the stomodæum, the pharynx. The term 'fulcrum' is now in general use; but it is not absolutely correct, as it is applied to a part of the mouth of the Hymenoptera which has a different morphological value.

Between the cephalo-pharynx and the great hooks of the blow-fly larva there is a second sclerite, which is developed in relation with the orifice of the salivary duct and ligula; it articulates behind with the cephalo-pharynx, and in front with the great hooks. This is the 'connecting piece' of Weismann. I shall term it the hypostomal sclerite, owing to its position in the floor of the mouth.

Above the hypostomal sclerite, in each lateral wall of the mouth, there is a short rod of chitin, which abuts upon the fulcrum behind; I shall term it the parastomal sclerite.

**The Cephalo-pharyngeal Sclerite** may be described as consisting of two vertical plates united by a thin dorsal arch. Each lateral plate exhibits three processes—an anterior inferior, a posterior inferior, and a posterior superior process. The latter I shall term the cornu.

In the newly-hatched larva these processes are very slender (Fig. 9, *1*), but after the second moult they become exceedingly thick and strong.

The cornua consist, in the adult, partly of dark and partly of transparent chitin; they exhibit thick upper edges, which lie in close proximity, so that they enclose a cavity, which contains a blood sinus and the dilator muscles of the pharynx. I shall speak of this cavity as the pharyngeal sinus.

**The Hypostomal Sclerite**† is H-shaped in the adult larva; its posterior processes articulate with the anterior inferior processes of the cephalo-pharynx, and its anterior processes support the great hooks. I have been unable to find any trace of this sclerite before the second moult.

\* Macloskie, G., in a preliminary note on the head of larval Muscæ, held views which are very similar to my own. 'Psyche,' Vol. iv., p. 218, Cambridge, Mass., 1884.

† 'Zungenbein' of Schröder v.d. Kolk. 'Mémoire sur l'Anatomie et Physiologie du Gastrus Equi.' Verhand. d. kl. Nederl. Inst., Bd. ii., pp. 1-155, 13 pl., 1845.

The Labral Sclerite of the newly-hatched larva (Figs. 7, *m*, and 9, *z, m*) articulates by a pair of processes with the anterior inferior processes of the cephalo-pharynx; these form the edges of the true mouth.

The Great Hooks (Fig. 9, 3, *h*) present three processes: a head which articulates with the hypostomal sclerite, a coronoid process above, which gives insertion to the retractor muscle, and a discal process below, which is adherent to the centre of the stomal disc.

In the adult larva a pair of small sclerites are found lying side by side in front of the crossbar of the hypostomal sclerite; they are the points of insertion for the retractor muscles of the labium.



FIG. 9.—1, the cephalo-pharynx and mouth armature of a newly-hatched larva; 2, the mouth armature of the same, seen from its ventral surface; 3, the same parts from the adult larva seen in profile; 4, a diagrammatic section through the thickest part of the cephalo-pharynx; 5, the head capsule of *Peciclostola*, after Brauer; 6, the internal head skeleton of the *Cossus* larva, after Lyonet—*m*, median; *h*, lateral hooks; *pt*, pseudo-tracheæ; *pl*, pseudo-labrum and discal sclerites; *x*, parastomal; *y*, hypostomal, sclerites; *cl*, clypeus; *z'* and *z''*, Zopfgräten or cephalo-pharyngeal processes; *f*, lateral plate; *iph*, pharyngeal sinus and muscles of the epipharynx.

The pharynx (Figs. 8 and 9, *4*) lies between the inferior processes of the cephalo-pharynx. In transverse section its cavity appears nearly crescentic. The concavity of the crescent is filled by the pharyngeal sinus; its lower wall is formed by a plate developed in the cuticle of the alimentary tube, the hypopharynx. The upper surface of the hypopharynx exhibits a series of longitudinal T-shaped ridges, which project into the œsophageal tube.

The dilator muscles of the gullet are inserted into the middle of the lower wall of the pharyngeal sinus, the epipharynx, and by their contraction dilate the alimentary tube, so that the food is sucked into it. When they relax it is depressed on the hypopharynx by its elasticity, like the plunger of a pump; by this means the food is driven into the crop. As there are no valves to the pharyngeal apparatus, I suspect the plunger itself acts as a valve, its anterior portion rising and descending before the posterior portion, so that the food is swallowed by a

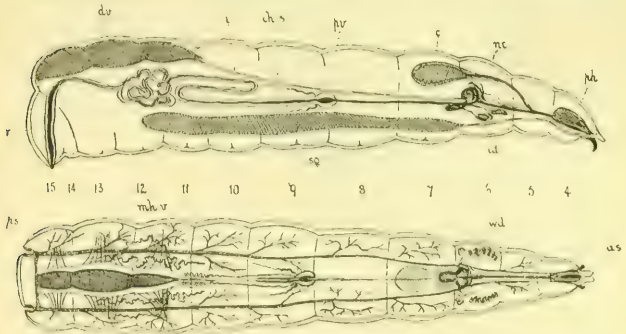


FIG. 10.—A vertical and horizontal diagrammatic section of the larva, to show the relative position of the internal organs and the segments. The segments are numbered on the supposition that the three cephalic post-oral somites exist. *as*, anterior spiracle; *ph*, pharynx; *id*, imaginal discs; *wd*, wing disc; *nc*, nerve centre; *c*, crop; *pv*, proventriculus; *ch*, chyle stomach; *i*, haemal curve of the intestine; *sg*, salivary gland; *dv*, dorsal vessel; *mhv*, Malpighian vessels; *ps*, posterior spiracle; *r*, rectum. The lower figure shows the general arrangement of the larger tracheæ.

kind of peristaltic act. The action of this organ is exactly similar to that of the fulcrum (pharynx) of the imago. The suctional action of the pharynx of the larva of *Cæstrus* was first pointed out by Scheiber [21]. The upper and back part of the pharyngeal sinus of the young larva lodges the antennal disc sac. In the adult larva this is placed behind the cephalopharynx, but it sends a pair of processes into the pharyngeal sinus, between the cornua and the inferior processes, in which the imaginal rudiments of the fulcrum of the fly are developed.

## 4. THE RESPIRATORY ORGANS.

The tracheæ of the larva consist of two main longitudinal trunks (Fig. 10), which give off numerous lateral branches. These divide and subdivide, and their terminal divisions form a dense network of exceedingly fine tubes, tracheal capillaries, in the peritoneal investment of the various internal organs.



FIG. 11.—Details of the tracheal system of the adult larva. 1, a section through the posterior spiracle,  $\frac{1}{2}$ -inch objective; 2, a section through one of the stigmatic slits ( $\frac{1}{2}$ -inch oil immersion); 3, section through the anterior spiracle ( $\frac{1}{2}$ -inch oil immersion); 4, a portion of a tracheal trunk,  $\frac{1}{2}$  objective; 5, tracheal terminations—*p*, peritracheal cells (*peritoneal coat*); *tr*, trachea; *v*, vestibule; *s*, slits; *n*, nuclei of peritracheal cells; *c*, mesoblast cells; *pr*, fibres of the vestibule—*g*, grating of the slits; *id*, imaginal disc of the anterior spiracle (upper prothoracic disc).

Leydig\* correctly maintained that these capillaries are developed in the interior of the cells of the connective tissue, but Wistinghausen† has quite recently described them as between

\* Leydig, Fr., 'Zum Feineren Bau des Arthropoden.' Müller's Archiv., 1855.

† Wistinghausen, 'Über Tracheenendigungen in den Sericterien der Raupen.' Zeitsch. f. w. Zool., Bd. 49, p. 565.

the cuticular tunica propria and the cells in the silk-glands of caterpillars, a view from which I must dissent; from his figures I conclude that his tunica propria is the peritoneal coat, and that the capillaries do not perforate the basement membrane as he supposes. I have never found any instance of such a disposition; they are everywhere confined to the mesoblast, and neither perforate the myolemma of the muscle fibres nor penetrate between the epithelial elements of the hypoblast or epiblast.

No organs undergo so many changes during the life of the larva as the arborescent tracheæ; in the newly-hatched insect they are few, but increase rapidly in number as growth progresses, until at length every organ, except the fat bodies, is richly supplied with a network of tracheal capillaries. Before the first moult the main tracheæ communicate with the exterior by a single pair of stigmatic slits on the fourteenth segment. After this, at first two, and then three, such slits are found in each posterior spiracle, and a second pair of spiracles appear on the fourth or prothoracic segment, at the second ecdysis. It is usual to speak of the larvæ of the Muscidæ as being in the first, second, or third stage of development in relation to the number of slits in the posterior spiracles.

**The Structure of the Tracheæ** (Fig. 11, 4).—The main trunks and larger vessels exhibit an external coat of thin polygonal cells closely united by their edges. Indeed, in some preparations the boundaries of the cells are not visible, so that the tracheæ appear to be covered by a continuous layer of nucleated protoplasm, and were so described by Weismann [2, p. 117]. This appearance is, however, delusive, and the edges of the individual cells are perfectly distinct in properly preserved preparations. These cells do not exhibit indications of division, and increase in size with the growth of the larva, like the cells of the hypodermis. In the largest tracheal trunks of the adult larvæ they measure from  $60\mu$  to  $80\mu$  ( $\frac{1}{16}$  inch) in diameter. Internally to the cells there is a thick cuticular intima, with a distinct spiral structure, which gives the vessels their well-known appearance. Sections do not show a spiral thickening of the cuticular membrane.

In the smaller tracheæ the intima is apparently structureless, and these end in capillary vessels of from  $2\mu$  to  $3\mu$  in diameter in the interior of stellate or fusiform mesoblast cells (Fig. 11, 5). The development of the finer tracheæ in the interior of cells attached to the external coat of the larger vessels was first observed by Weismann [2, p. 220]. It will be seen that there is a striking similarity between the manner in which the tracheal capillaries of insects and the blood capillaries of vertebrates are developed by intracellular vascularisation.

Whether the cuticular intima is continued into the smallest tracheal vessels is doubtful, and the branching corpuscles in which these terminate have been, I believe, frequently described as plexuses of ganglion cells. They are not readily distinguished when they do not contain air, and the air is rapidly absorbed from them after death by the blood of the insect. They are more easily stained than nerve corpuscles by aniline dyes, and retain the colour longer when washed in water or dilute spirit. Wistinghausen (*l.c.*) speaks of these stellate cells as a terminal capillary network (*Endnetz*), and regards all the cells as vessels.

**The Posterior Spiracles** of the adult larva are situated in a pair of nearly round chitinized plates of a dark-yellow colour. Each presents three oblique transverse slits, partially closed by a fine chitinous grating. A vertical section through the stigmatic plate at right angles to the slits is represented in Fig. 11, 1 and 2.

It will be seen that each stigmatic plate is surrounded by a ring of chitin, the peritreme (Fig. 11, *pt*), which involves nearly the whole thickness of the external cuticle. The inner surface of the cuticular epidermis is covered with a cuticular network of fine fibres, extending across the interior of the slits and forming the grating (Fig. 11, 2).

Immediately within the spiracle there is a distinct cavity (*v*), lined by a similar cuticular network (*pr*); I shall term this cavity the vestibule of the trachea. Its intima resembles the external cuticle, and is quite unlike the proper intima of the tracheal vessels which open into it.

The tracheæ are usually regarded as derived from a tubular

involution of the epiblast. This does not appear to me to be the case; it is only the vestibule which is so formed, the tracheal trunks arising in the mesoblast as solid cell strings, a fact known to Weismann [2, p. 76]. This mode of development is more consistent with the fact that in some aquatic larvæ there are no spiracles, the tracheæ being closed.

The changes of form in the posterior spiracle which occur, when the larva moults, are not due to a modification of the spiracle, but to the formation of a new stigmatic plate on the outer side of the old one, from the hypoderm cells of the vestibule. The intima of the trachea separates from the external cellular layer, and a considerable space appears between them, which is filled with fluid. A new intima is then formed externally to the old one, the latter is afterwards shed with the stigmatic plate and the other cuticular structures, and the fluid is either absorbed or discharged.

The **Anterior Spiracles** (Fig. 11, 3) are developed before the second moult, and can be recognised beneath the epidermis of the very young larva as papillæ on the prothoracic segment. In the adult larva the anterior spiracle is fanlike: it presents about thirteen minute orifices. These communicate by short tubes with the tubular cavity of the spiracle, which is apparently entirely filled with minute granules, forming a close yellow spongy mass. I am inclined to regard this spiracle as functionally inactive, and it is difficult to understand how it could be otherwise, as it is usually buried in the decomposing fluid on which the animal feeds.

Its base is surrounded by the imaginal disc from which the spiracle of the nymph is developed (Fig. 11, 3, *id*).

## 5. THE CUTANEOUS MUSCLES.

The somatic or skeletal muscles of insects are all cutaneous. In the larva of the blow-fly they closely resemble those of other vermiform larvæ, and form a tolerably continuous sheet beneath the hypodermis. Two principal sets are easily distinguished; transverse fibres which extend from the lateral line (Fig. 4, *a*) towards the dorsal and ventral surface of the worm, some

passing obliquely forward and others backward, and a set of dorsal and ventral longitudinal muscles, the dorsal and ventral recti. These two sets are antagonistic to each other, the transverse fibres diminishing the diameter and increasing the length of the larva, and the recti drawing the annuli together.

The individual fibres and bundles of cutaneous muscles would need many pages for the description of their origins and insertions, and the details possess little or no interest. Lyonet has already described the similar muscles of the caterpillar of the goat moth; I shall, therefore, content myself with a very brief *résumé*.

Generally all the muscles are attached to the integument where more or less obvious sulci are apparent externally, and the muscles of each annulus are repeated in the others; most of the fibres pass from the edge of one annulus to that of the next, but some pass over two or more without being attached to the integument.

The muscles of the cephalo-pharyngeal skeleton must be regarded as an inflected continuation of the cutaneous sheet; the fibres and bundles of fibres are chiefly the continuation of the recti: these form special retractors and protractors of the fulcrum, or act upon the labium and the great hooks. The great retractors of the fulcrum arise from the anterior edge of the sixth somite, whilst the protractors arise from the forehead and maxillæ. This fact is a complete refutation of the view held by Hammond,\* that the delimitation of the several somites can be determined by the insertions of the somatic muscles.

In structure the larval muscles generally differ from those of the imago, and they more nearly resemble the skeletal muscles of vertebrates; a detailed description will be given in another chapter.

## 6. THE ALIMENTARY CANAL.

### a. Comparative Morphology.

The Alimentary Canal in insects consists of four parts: the stomodæum and proctodæum, developed from the epiblast;

\* 'On the Thorax of the Blow-fly.' Journ. Linn. Soc. Zool., vol. xv., 1879.

and the mesenteron and metenteron (*mili*), developed from the hypoblast.

The terms which have been applied to its several sections are such as indicate incorrect homologies with the alimentary canal in vertebrates. The stomodæum consists of the pharynx, œsophagus, crop, and of a portion of the proventriculus.

**The Crop.**—This is the sucking stomach of Weismann; it is more properly termed a food-sac. In manducatory insects the term is applied to a uniform enlargement of the œsophagus, which in phytophagous Orthoptera and Coleoptera frequently occupies nearly the whole thorax and a considerable portion of the abdomen. In suctorial insects the crop is a diverticulum of the ventral surface of the œsophagus, usually with a long tubular neck. The neck of the crop often appears as the direct continuation of the gullet, whilst the second part of the œsophagus ascends almost at right angles to the first, and enters the proventriculus.

In the imago in the Diptera, Hymenoptera, and Lepidoptera the crop is the well-known honey-bag; it is situated in the abdomen, and when distended with food occupies a considerable portion of that cavity.

**The Proventriculus** of suctorial, corresponds with the gizzard of manducatory insects; it is usually a thick-walled, almost

#### DESCRIPTION OF PLATE I.

FIG. 1.—The Alimentary Canal of the Adult Larva, 3-inch objective: *pv*, proventriculus; *c g*, cæcal glands; *ch*, chyle stomach; *i*, proximal, and *i'*, distal intestine; *mp*, Malpighian vessel; *r*, rectum; *tr*, tracheæ.

FIG. 2.—Section of a Portion of the Crop,  $\frac{1}{4}$ -inch objective: *cu*, cuticle; *ep*, epithelial cells; *pl*, peritoneal coat; *g*, ganglion cells.

FIG. 3.—Proventriculus: *mn*, median, or stomogastric nerve; *g*, proventricular ganglion; *cg*, gastric cæca; *ch*, chyle stomach.

FIG. 4.—A Longitudinal Section through the Proventriculus: *a*, œsophagus; *tr*, trachea; *i d*, imaginal disc; *pv*, proventriculus; *ch*, chyle stomach.

FIG. 5.—Transverse Section through one of the Gastric Cæca,  $\frac{1}{4}$ -inch objective.

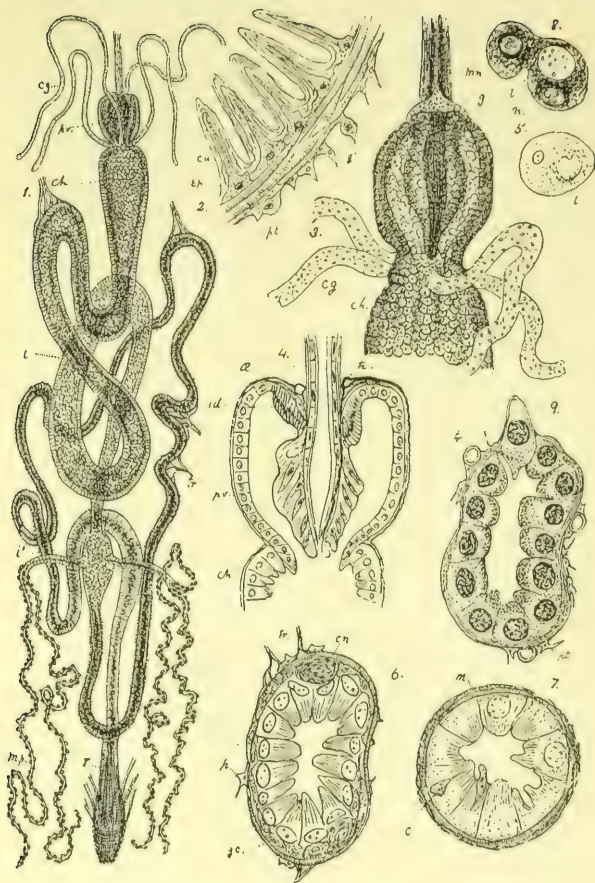
FIG. 6.—Transverse Section through the Chyle Stomach; *c n*, cell nests; *gc*, parietal cells.

FIG. 7.—A Transverse Section through the Distal Intestine,  $\frac{1}{4}$ -inch objective: *c*, amœboid cells.

FIG. 8.—Transverse Section of a Malpighian Tube,  $\frac{1}{4}$ -inch objective.

FIG. 9.—Transverse Section of a Salivary Gland of Resting Larva, showing the formation of the Membrana Propria.

# PLATE I.



THE ALIMENTARY CANAL OF THE LARVA.



spherical organ, formed by the invagination of the posterior extremity of the stomodæum in the anterior portion of the mesenteron. When it assumes the form of a gizzard, the œsophageal portion is lined by a series of radially symmetrical chitinized folds, which form an efficient organ for the trituration of the food. The form of the proventriculus in the fly is typical of that in all suctorial insects.

The **Mesenteron** consists of the chyle stomach and its appendages, and of that portion of the intestine in front of the Malpighian tubes. Some authors have named the whole of this part of the alimentary canal the chyle stomach. Although there is no distinct line of demarcation between the anterior and posterior portions of the mesenteron in many insects, the two sections of the tube differ considerably, and in some forms are distinctly divided by a pyloric sphincter into a chyle stomach and an intestine. I shall therefore use the term proximal intestine for the posterior portion of the mesenteron.

The **Metenteron** begins in front of the orifices of the Malpighian vessels, as a distinct thin-walled dilatation of the intestine (Pl. I., Fig. 1), the lower part of which forms a large diverticulum or cæcum in many insects. Beyond this the intestine is much narrowed, and exhibits a thick muscular coat. I shall term it the *distal intestine*, and shall speak of the dilatation as the *sinus*. This distal intestine is termed the ileum or colon by different writers.

The rectum or proctodæal involution has a very distinct structure, and is always lined by a thick cuticular intima; it is usually separated from the metenteron by a valve, which is formed by its invagination within the metenteron; the valve is not unlike the proventriculus in the disposition of its walls.

The **Glandular Appendages** of the alimentary canal are known as the salivary and gastric glands, the Malpighian vessels, and the rectal glands.

**The Salivary Glands.**—This term is applied to all those glands in insects which discharge their secretion into the mouth or pharynx. The largest and most constant have a duct, which

opens at the tip of or under the ligula. In many insects they secrete a true digestive fluid, with proteolytic or amylolytic ferments; in others they are silk glands (sericteria). I shall term them lingual glands, a term which is equally appropriate whatever their function.

The other salivary glands may be distinguished as accessory lingual, labial, oral, or pharyngeal glands, according to the position of the orifices of their ducts.

Moseley regards the lingual glands as modified cutaneous glands, homologous with the tracheæ. They are certainly developed as involutions of the epiblast at the root of the second pair of maxillæ, but differ in their mode of development from the tracheæ. The only reason for considering that they are homologous with the latter is the spiral structure of the intima of their duct.

**The Gastric Glands**, or gastric cæca (Pl. I., Fig. 3, *cg*) are tubular glands arising from the walls of the chyle stomach. They are frequently very numerous, but as often entirely wanting.

**The Malpighian Vessels** are simple or branched tubules, containing large cells, which give them a moniliform appearance. In some insects they are very numerous. In most, if not in all, Diptera there are two, each dividing into two tubes (Pl. I., Fig. 1, *mp*). I know no insect in which they are entirely absent. Malpighi supposed these tubes to be hepatic; Leydig and most modern writers consider them renal. This view I shall show hereafter is not consistent with facts; and, in spite of the weight of authority, I strongly incline to the theory of Malpighi.

**The Rectal Glands** are situated in the proctodæum. They are frequently wanting, and apparently exhibit great variations in different insects. In the larva of the fly they are entirely absent. In the perfect insect I think they are undoubtedly concerned in the excretion of a substance allied to, but not identical with, uric acid.\*

\* The functions of these and of the other internal organs will be fully discussed in the physiological section of this work.

### b. The Alimentary Canal of the Blow-fly Larva.

**General Structure.**—The wall of the whole alimentary tube exhibits a peritoneal, a muscular, and an epithelial coat.

**The Peritoneal Coat** (Pl. I., Figs. 2, *pt*, and 6, *p*) is the most external. It consists of stellate mesoblastic cells, endothelial plates, and tracheal vessels; it forms part of the wall of a great blood sinus, which surrounds the whole alimentary tract.

**The Muscular Coat** consists of two layers, an external longitudinal and an internal circular set of striated fibres. Those of the pharynx and rectum resemble the somatic muscles; but the remainder of the muscular coat consists of flat branching bands of less distinctly striated fibres, without any myolemma, which do not exceed  $8\mu$  to  $10\mu$  in their broadest transverse diameter.

**The Epithelial Coat** consists of flat polygonal cells in the stomodæum and proctodæum, and of cubical or columnar cells in the rest of the alimentary tube. In the stomodæum and proctodæum there is also a thick cuticular intima; in the mesenteron this intima is either absent or much thinner, but the cells secrete a mucoid layer on their inner surface. In the larvæ of some Nematocera, however, a distinct cuticular lining can be seen in the living animal, separating the coarser particles of food from a clear fluid, which intervenes between the cuticle and the epithelium. Hammond [24] describes the same thing in the chyle stomach of the Crane-fly larva.

It appears to me that the difference between the mesenteron and the stomodæum and proctodæum does not consist in the absence of a cuticular layer in the former, but in its non-adherence to the cells. In the anterior and posterior sections of the gut the cuticular intima is only shed at an ecdysis, whilst that of the mesenteron is shed during digestion, and probably only forms a net-like mucoid envelope around the coarser particles of food material.

**Basement Membrane.**—There is a very thin cuticular membrane between the epithelial cells and the muscular coat; and

these cells are firmly cemented together at their base, although they are quite separate towards their apices. The nature and origin of the basement membrane is more apparent in the lingual glands, where it forms the tunica propria.

The *Œsophagus* commences at the posterior inferior part of the fulcrum, and extends backward, as a narrow cylindrical tube, to the posterior border of the ninth segment (Fig. 10). Close to its anterior extremity it gives off a diverticulum on its ventral surface, the neck of the crop, or, more properly, of the food sac; it then passes between the crura of the supra-*œsophageal* ganglia or hemispheres, lies above the ventral ganglia, and terminates in the proventriculus.

The length and diameter of the *œsophagus* and the position of the proventriculus varies with the condition of extension or contraction of the anterior segments of the larva. The figure represents a fully-extended larva; in the contracted state the proventriculus lies close behind the ganglia.

**The Crop.**—The neck of the crop has about the same diameter as the *œsophagus*. After a short course towards the ventral surface, it curves upwards on the left side towards the back, and dilates into a large sac, which lies over the nerve centres and dorsal vessel. It can be distinctly seen in the living larva through the skin, as it is usually filled with dark gray decomposing fluid; when distended, it occupies the dorsal region of three or four segments.

The epithelial coat of the *œsophagus* and crop consists of flat cells, and is separated from the lumen by a thick laminated, cuticular layer, which is deeply plicated, processes from the cells extending into the cuticular folds (Pl. I., Fig. 2). When the organ is distended, the folds are obliterated, so that the epithelium has clearly an amœboid character. When these viscera are contracted, the plicated cuticle may fill the whole interior.

The under surface of the crop has a large group of ganglion cells spread over it—the ‘ganglion of the crop.’

**The Proventriculus** (Pl. I., Figs. 3 and 4) is ovoid, its long axis corresponding with the axis of the body. A longitudinal

section through the proventriculus shows that it consists of three layers, the outermost continuous with the wall of the chyle stomach, and the innermost with that of the œsophagus. By traction the œsophagus can be drawn out with the intermediate layer, demonstrating that the organ is formed by an intussusception or intrusion of the œsophagus within the mesenteron.

Tracheal vessels and mesoderm cells pass into the space between the inner and intermediate layers of the proventriculus; and the œsophagus is surrounded by a tracheal ring, from which these vessels arise, with twelve others, which course over the exterior of the proventriculus and chyle stomach.

The epithelium, in the interior of the proventriculus, is divided into two regions by a distinct ring of embryonic cells (Pl. I., Fig. 4, *id*), which is destined to develop in the nymph into the proventriculus of the imago. I shall term it the proventricular ring. The cells of the external wall are cubical; those of the internal wall exhibit a peculiar feathered appearance, and are not unlike the epithelium of the human stomach.

Kowalevski\* regards the proventricular ring as the rudiment of the stomodæum of the nymph. This is an error, due to the prevalent view that the whole of the proventriculus is stomodæal. I shall hereafter show that it forms the proventricular epithelium only.

A large crutch-shaped ganglion (Pl. I., Fig. 3, *g*), the *proventricular ganglion*, lies in the angle between the dorsal surface of the œsophagus and the proventriculus, at the posterior end of the stomogastric (*median*) nerve; ganglionated fibres pass from it into the wall of the proventriculus and chyle stomach.

**The Chyle Stomach** (Pl. I., Figs. 1, 3 and 6), is 3 mm. long, and broader in front than behind. It has four tubular cæcal glands at its anterior end. These glands measure about 2 mm. in length, and resemble the chyle stomach in structure. They do not reappear in the imago. Its epithelial coat consists of

\* 'Beiträge zur Kenntniss der Nach-Embryologie der Musciden.' Zeitsch. f. w. Zool., Bd. xlv., 1887.

large conical cells, of from  $20\mu$  to  $30\mu$  in diameter, which are often  $80\mu$  from base to apex, with large ovoid nuclei. These cells are distinctly striated towards its lumen (Pl. I., Fig. 6); there is also a layer of sub-epithelial or parietal cells (*gc*), which are probably glandular, and a large number of very remarkable cell-nests (*cn*) are scattered between the epithelial and muscular coats. They are formed of small flattened cells,  $5\mu$  to  $6\mu$  in diameter, arranged in concentric layers. They are most numerous in the chyle stomach, and are found in the proximal intestine. They are absent in the gastric cæca. These curious bodies are apparently the histoblasts from which the mesenteron of the nymph and imago are developed.

**The Proximal Intestine** is 9 mm. long ( $\frac{3}{8}$ ths of an inch). After making a dorsal flexion forwards (*the hæmal flexure*), it passes backwards (Fig. 10), and forms several coils in the twelfth segment. It becomes much narrowed, and terminates in the sinus.

There is a distinct ring of embryonic cells which surrounds the sinus at the orifices of the Malpighian vessel. This Kowalevski regards as the rudiment of the proctodæum of the imago. I consider it the rudiment of the metenteron, which was unknown to Kowalevski.

The muscular coat of the chyle stomach and proximal intestine has the appearance of a lattice-work, with considerable spaces between the fibres; that of the sinus is very thin.

**The Distal Intestine** (Pl. I., Fig. 1, *i'*) is chiefly coiled up with the proximal intestine and the vessels of Malpighi in the twelfth segment. It measures 18 mm., or  $\frac{1}{8}$ ths of an inch, in length. It is very narrow and has a thick muscular wall, which consists chiefly of circular muscle fibres. Its epithelium has a clear mucoid character, and amœboid corpuscles are seen within and between the cells (Pl. I., Fig. 7, *c*), which frequently exhibit goblet degeneration.

**The Rectum** is not more than 1 mm. ( $\frac{1}{25}$ th of an inch) in length, and descends almost vertically from the dorsal towards the ventral aspect of the larva. The epithelium is flat, and is covered internally by a thick longitudinally plicated cuticle. The

epithelial cells send processes outwards into the muscular coat. The muscular coat is from 20 $\mu$  to 25 $\mu$  thick, and towards the anus has a strong sphincter, composed of from 20 to 30 circular fibres. Numerous muscle-fibres arise from the integument on either side, and pass inwards and downwards, to be inserted into the peritoneal coat of the rectum by fine tendon-like ends. All the muscle-fibres of the rectum resemble the skeletal muscles of the imago, and each exhibits a close row of central nuclei (see Histology and Histolysis of the Larval Tissues). The limits of the distal intestine and the rectum are not distinctly defined, but the cuticular intima of the latter becomes thinner, and the epithelium exhibits a transitional character towards the distal intestine. In the imago the two are separated by a valve.

**The Tracheæ of the Alimentary Canal.**—The great lateral tracheal trunks give off one or more branches on each side in each segment to the alimentary canal. The largest branches are those to the proximal intestine. Two very large trunks join the intestine at the anterior part of the hæmal flexure and retain it in its place; the other large tracheæ enter the intestinal coil and bind it together. These also send numerous capillary branches to the Malpighian tubules.

**Intestinal Ganglia.**—Viallanes [27, p. 74] describes a distinct plexus of stellate ganglion cells in the muscular coat arranged in four parallel rows, and extending the whole length of the chyle stomach and intestines of the larva of *Tipula gigantea*. I have been quite unable to find any such structure in the larva of the Blow-fly, but no doubt ganglion cells derived from the proventricular ganglion exist.

**Visceral Muscular Network.**—Weismann [2] has described a network of delicate muscle-fibres, which connect the walls of the alimentary canal with the alæ of the dorsal vessel; but I have been unable to detect any such fibres, and, if they really exist, they could scarcely fail to appear in some of my numerous sections.

**The Lingual (Salivary) Glands** are a pair of very large sac-like glands, which consist of a thin cuticular membrane, covered

externally by a reticulum of stellate mesoblast and tracheæ, and lined by a very regular pavement epithelium consisting of large hexagonal cells. These glands, in the recent condition, are most beautiful microscopic objects. They lie one on either side of the alimentary canal, and measure nearly a centimètre in length, and '6 mm. in diameter in their widest part. Each has a narrow duct, which joins its fellow beneath the pharynx. The conjoined duct opens through a papilla, which represents the ligula (Figs. 7 and 8):

The condition of the secreting cells varies greatly at different periods. In the young larva the cells are small and increase in size with the growth of the insect. In the active feeding adult they measure 100 $\mu$  to 150 $\mu$  in diameter, and form a thin pavement 25 $\mu$  thick, enclosing a large cavity, which is filled with clear fluid. In the resting larva the cells rapidly increase in thickness, until at length they reduce the cavity of the gland, so that it appears as a mere stellate fissure in sections. In this condition they are cubical.

A chitinous or cuticular intima between the cells and the lumen of the gland has been frequently described in the salivary glands and sericteria of various insects. In the active gland in the fly larva I find no trace of such a membrane, but in the resting larva a thin cuticular intima is often present.

The gland-cells exhibit many exceedingly interesting appearances. They have a distinctly reticular structure. Their vesicular nuclei can often be separated in the recent condition of the organ. In the resting larva the cells still have numerous granules of secretion towards their inner surface, and are firmly united externally, where they have a distinctly laminated structure, the laminæ passing from cell to cell, an indication that the lamellated cuticle is formed from the cells themselves, and not by a secretion poured out on their surface (Pl. I., Fig. 9).

Towards the gland-duct the cells are considerably reduced in magnitude, and in the duct itself they form a cuticular intima on their inner surface, which exhibits a spiral thickening similar to, but coarser than, that of the tracheal vessels.

A ring of embryonic cells intervenes between the cells of the

gland-sac and its duct. This, according to Kowalevski, is destined to develop the corresponding gland in the nymph.

The salivary glands of insects have attained a classical interest, owing to the various researches which have been made on the nerve terminals and their relation to the secreting epithelium. In the fly larva their nerves are derived from the proventricular ganglion, which gives off numerous short nerves, ending in the salivary cells. It appears to me that these are processes of the ganglion directly continuous with the protoplasm of the secreting cells, and that only a few of the cells—those adjacent to the ganglion—receive any.

Weismann described a very remarkable structure, which he calls a cell chaplet, connected with the external coat of the two salivary glands. He says:

‘It consists of a string of large cells closely united, which hangs like a garland free in the body cavity. Its two ends are connected with the salivary glands, and with a muscular band from the dorsal vessel. It forms an arch, with its convexity directed backwards, in the horizontal plane near the back. This string of cells has no duct.’ [2, p. 132.]

**The Malpighian Vessels** are two in number, but each divides into two tubules about two mm. from its junction with the intestine. I cannot give the length of these tubules accurately, as they are not easily unravelled, but it is considerably more than a centimètre. They are at once recognised by their dark brown colour, and they become intensely black when treated with osmic acid.

The Malpighian tubes have no muscular coat; but consist of a structureless external cuticle, lined with a single layer of cells, two, or at most three, cells entirely surrounding the tube (Pl. I., Fig. 8).

Externally they exhibit a moniliform appearance, the large cells projecting as hemispherical protuberances on the surface. The lumen of the gland is small and irregularly flattened. The cells measure 70 $\mu$  to 80 $\mu$ , and have large, nearly spherical nuclei.

The cell protoplasm is distinctly reticular, and contains

numerous granules of dark brown pigment, of a substance deeply blackened by osmic acid, and of a colourless material which stains with carmine, but is unaffected by osmic acid. Normally there are no crystals, either in the cells or in the secretion, although some preparations exhibit crystals which resemble stearin or tyrosin. These are apparently the result of post-mortem changes.

## 7. THE NERVOUS SYSTEM.

### a. Comparative Morphology.

The nervous system in insects consists of two parts, a somatic and a splanchnic system of nerves and ganglia, which have been properly compared with the cerebro-spinal and sympathetic systems of the vertebrata, respectively. The former supplies the integument, the organs of special sense, and the skeletal muscles; and the latter innervates the visceral muscles, and probably has a trophic influence on the secretory epithelia.

The somatic nervous system consists of a series of ventral ganglia, united with each other by one or two longitudinal commissures. In the primitive embryonic condition all the ganglia are distinct, and there may be as many as seventeen pairs—four cephalic, three thoracic, and ten abdominal (Brandt [30]). As development progresses, several of the ganglia become fused together, and this fusion is more marked in the higher types of insects. Most larvæ have only two centres in the head, a pre-oral and a post-oral centre, with three thoracic and seven or eight abdominal ganglia. In the imago, the two cephalic centres are frequently fused, and the thoracic form but two centres. The greatest concentration occurs in the Muscidae, which have only two centres in the imago, the cephalic and

#### Bibliography :—

28. NEWPORT, G., 'On the nervous system of the larva of *Sphinx ligustri* and the changes it undergoes in the earliest stages of the pupa.' *Phil. Trans.*, 1832, p. 383. London.
29. BRANDT, E., 'Vergleichend. Anatomische Skizze des Nervensystems der Insekten.' *Horæ Soc. Ent. Ross.*, tom. xv., 1879.
30. BRANDT, E., 'Ueber die Metamorphosen des Nervensystems der Zweiflügler.' *Horæ Soc. Ent. Ross.*, tom. xv., 1879.

thoracic, whilst in the larva all are united in a single complex nerve-mass, in which no trace of the primitive separation of the post-oral ganglia remains perceptible externally.

The anterior pair of cephalic centres is always pre-oral, and is developed from the pro-cephalic lobes. In the perfect insect it consists of a central pair of hemispherical ganglia, having a more or less convoluted surface united by a commissure. These support two pairs of pedunculated bodies—the corpora fungiformia—as well as two pairs of sensory ganglia, the optic and olfactory (antennal) lobes. These structures are usually known as the ‘brain,’ but the term is more conveniently applied to the whole of the cephalic ganglia whenever they are united into a single cephalic centre, and when this is the case the commissures which unite the supra- and infra-œsophageal centres are called crura, and are not usually visible externally.

The first post-oral centre, or the infra-œsophageal ganglion, usually consists of three primitive ganglia united; these belong to the segmented portion of the head, the mandibular, maxillary and labial somites. In the Diptera the first pair are apparently wanting in both the larva and imago.

In the Hymenoptera and Coleoptera, three pairs of nerves are given off from these ganglia; in the Diptera and Muscidæ there are only two pairs, whilst the Lepidoptera have only a single pair (Brandt [29]).

A small nerve arises, in most insects, from the commissure between the supra- and infra-œsophageal ganglia, on each side. These are usually known as the ‘labral’ nerves, but I prefer the term ‘pharyngeal’ nerves, as they supply the pharynx as well as the labrum—in the Diptera, at least.

The pharyngeal nerves give off a pair of recurrent branches which join the frontal ganglion of the splanchnic system (Pl. II., Fig. 2). These are the recurrent nerves; sometimes they have a separate origin distinct from that of the pharyngeal nerves. They are also described as arising from a special ganglion in the commissure—the ganglion of the commissure.

Each of the other segmental centres, those of the thorax and abdomen, except the last, usually consists of a single pair of

ganglia. The last is, however, evidently the result of the union of two or more pairs.

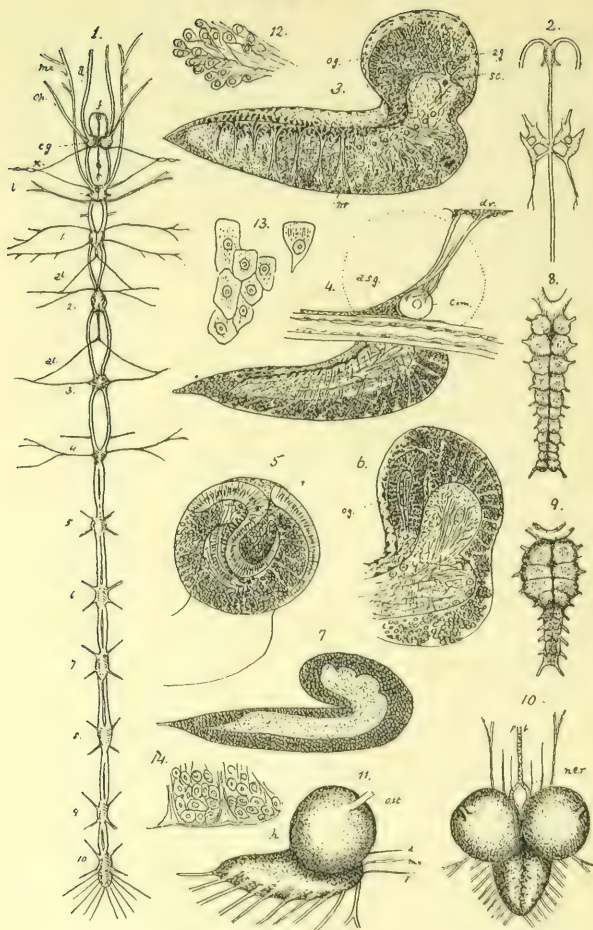
Each pair of ganglia gives off one, two, or three pairs of nerves, and in the latter case the third pair either arise from the commissures behind the ganglia, or from the posterior part of the centre by a common trunk. This trunk then bifurcates, and its branches unite with the anterior nerves of the succeeding ganglion (Pl. II., Fig. 1, *al*). They are the alary and lateral nerves of Newport [9], and are of considerable morphological and physiological interest, as their origin from the segmental centres is apparent rather than real, and they consist of fibres, which traverse the dorsal surface of the nerve centres and their commissures, and arise from the brain, so that these probably represent the voluntary motor tracts of a vertebrate. [Newport, 9.]

When the primitive ganglia are fused into one or a few complex centres, the determination of their exact number is exceedingly difficult. This is especially the case in the Diptera. Brauer [14] gives a very complete comparative table, showing the disposition of the primitive ganglia in the larva and imago of various dipterous types, in which he shows that there are always three thoracic and eight abdominal ganglia. I must, however, regard this table as hypothetical to a large extent—although there are obviously ten

PLATE II.—THE NERVOUS SYSTEM OF THE LARVA OF THE BLOW-FLY.

- FIG. 1.—The Ventral Chain of the Silk Moth Larva, after Swammerdam : *a*, antennal nerve ; *mx*, maxillary nerve ; *c g*, cephalic ganglion ; *op*, optic nerve ; *f*, frontal ganglion ; *x*, lateral ganglia? ; *i*, infra-oesophageal ganglion ; *al*, alar nerves. The ganglia of the thorax and abdomen are numbered 1 to 10.
- FIG. 2.—The Frontal and Lateral Splanchnic Ganglia of the Cockroach. After Hofer.
- FIG. 3.—A Longitudinal nearly Median Vertical Section of the Neuroblast : *a g*, antennal ganglion ; *s c*, stellate cell ; *og*, retinal disc ; *n r*, nerve roots.
- FIG. 4.—A Median Section of the same : *a s g*, anterior splanchnic ganglion ; *com*, commissure of hemispheres.
- FIG. 5.—A Section through the outer part of a hemisphere : *r*, retinal disc.
- FIG. 6.—A Section through the crus and hemisphere.
- FIG. 7.—A Longitudinal Lateral Vertical Section through the Neuroblast of the newly-hatched larva.
- FIG. 8.—The Ventral Ganglia of Melophagus, 1st Stage, after Leuckart.
- FIG. 9.—The Ventral Ganglia of Melophagus, 2nd Stage, after Leuckart.
- FIG. 10.—Dorsal View of the Neuroblast : *n e r*, ring.
- FIG. 11.—Lateral View of the same : *h*, hemisphere ; *o s l*, optic stalk.
- FIG. 12.—Nerve Cells from Nerve Root.
- FIG. 13.—Embryonic Cells of the Cortex of the Neuroblast.
- FIG. 14.—Embryonic Cells and Trabeculae of the Capsule of the Neuroblast.

# PLATE II.



THE NERVOUS SYSTEM OF THE LARVA.



pairs of ganglia in the Tipulidæ, of which the last is a complex of two pairs, and Leuckart figures eleven pairs in the embryo of the Pupiparæ at an early stage of development (Pl. II., Fig. 8). At a subsequent stage only nine remain—the penultimate and antepenultimate pair have disappeared (Pl. II., Fig. 9).

In the newly-hatched larva of the Blow-fly I have only detected evidence of the existence of six pairs, but ten pairs of nerves arise from the united ganglia.

It appears to me that the number is reduced, either by complete fusion of two or more, only in certain cases, and that in others the missing ganglia have undergone complete atrophy. As one centre often gives off at least two, and often three pairs of nerves, I do not regard the numbers of pairs of nerves as evidence of the persistence of a similar number of ganglia.

There are apparently never any ganglia developed in the last abdominal metamere—Weismann's twelfth segment, my fourteenth and fifteenth somites. Weismann demonstrates this in 'Chironomus' [2, p. 38], and adduces it as an argument against Zaddach's hypothesis that a pair of primitive ganglia is developed in each somite [2, p. 83].

**The Splanchnic Nervous System** (Pl. II., Figs. 1 and 2) was first detected and figured by Swammerdam [4], and has been carefully studied by J. Müller,\* J. J. Brandt,† Newport [9], and more recently by Bruno Hofer.‡ It is highly developed in the cockroach; and exhibits considerable modification, and attains great importance in the larva of the Blow-fly.

It consists of two single median and of two pairs of lateral principal ganglia.

The median ganglia are the frontal and proventricular; they are united by a single thick nerve-cord, which lies immediately upon the dorsal surface of the œsophagus. This is the median or stomogastric nerve.

The lateral ganglia consist of an anterior and a posterior pair. They are connected with the crura of the pre-oral centres, with each other, and with the stomogastric trunk by plexiform nerves, and they supply the labial salivary glands—(B. Hofer).

The nerves of the splanchnic system arise from these ganglia and from the stomogastric nerve, and terminate in

\* Nova Acta, K. L. C. Acad., Bd. xiv., p. 73.

† 'Oken's Isis,' 1831, p. 1103.

‡ 'Untersuchungen ii. den Bau der Speicheldrüsen u. d. dazu gehörenden Nervenapparats von Blatta.' Nova Acta, K. L. C. Acad., Bd. li., 1887.

ganglionated plexuses in the walls of the viscera, similar to those of Auerbach and Meissner in the vertebrata.

#### b. Structure of the Nerve Centres.

The somatic nerve-centres in all insects consist of a central stroma of fibrillated substance, which I regard as analogous to the network of Gerlach, surrounded by a vesicular layer, or 'gray substance.' This is enclosed in a thick capsule of mesoblastic tissue rich in tracheæ—the peritoneal capsule—continuous with the sheaths of the nerves.

The **Central Stroma** consists of a fine network of axis cylinders, permeated in many cases by distinct bundles of larger fibres—commissural fibres, and nerve roots.

Many of the nerves arise in part from this stroma, and in part from the peripheral nerve-cells. Some portions of the white substance are blackened very easily by osmic acid, and others are scarcely tinged by it. Those parts which become black are infiltrated by an interfibrillar substance of a fatty character. Dietl\* named this variety of the stroma 'Marksubstanz,' medullated stroma, or medullated substance.

The medullated substance has been a great difficulty in the investigation of the nervous system in insects. It often appears in sections as a homogeneous or laminated material, or in the form of solid balls, which have been mistaken for giant cells. Dietl correctly described this substance. He says: 'Like ordinary stroma, it consists of nerve fibrils, which vary greatly in size—from large distinct nerve-fibres, such as are found in nerves, forming commissural bundles, to the finest reticulum of minute axis cylinders, forming a dense stroma;' but he also says 'it sometimes exists as a homogeneous mass, or in the form of laminæ.'

Such homogeneous masses are, however, readily resolved into a stroma by treatment with a mixture of ether and chloroform, which dissolves a fatty interstitial substance. By this method they are seen to differ in no way from the parts in

\* Dietl, 'Die Organization des Arthropodengehirns.' Zeitsch. f. w. Zool., Bd. xxvii., 1876.

which the stroma is more apparent, except in the greater abundance of the infiltrating fatty material.

Dietl observes that the medullated stroma only resembles the white matter in vertebrates (the medullary sheath of Schwann) in its reaction with osmic acid. In this I am not inclined to agree with him ; it appears to me that the interstitial substance differs but little from the white substance of Schwann, and chiefly in not being differentiated into a distinct sheath around each fibre. I regard it as an interfibrillar substance, or matrix, in which the axis cylinders, whether bundles of larger fibres or fine stroma are imbedded. I shall distinguish the two forms of stroma as non-medullated and medullated stroma.

**The Gray or Cortical Substance** consists either of large or small ganglion cells.

The large ganglion cells are stellate with numerous branching processes, which are continuous with the stroma of the central white substance. Some of the processes are directly continuous with the nerves, but many of the nerve-fibres of the peripheral nerves arise from the stroma.

The small ganglion cells are chiefly found in the supra-œsophageal centres, and form a layer many cells thick. They are spherical nuclear corpuscles, surrounded by a very little protoplasmic cell substance, which is prolonged in a fine fibre, and unites these cells in strings or chaplets, ultimately becoming continuous with the central stroma. The small round cells resemble those of the nuclear layers of the cerebellum and retina in vertebrates.

The external capsule, or peritoneal coat, varies greatly in thickness ; but differs in no way from the mesoblastic tissue covering the other internal organs.

#### c. The Somatic Nervous System and the Neuroblast of the Blow-fly Larva.

The central nervous system in the larva of the cycloraphic Diptera generally, differs widely from that of other insects in the close concentration of all the ganglia in a single complex centre, which consists in part of the differentiated nervous

system of the larva, and in part of embryonic structures destined to form the nerve centres in the nymph.

Although these parts are intermixed in a complex manner, the cellular elements of each are distinctly recognisable, and those which are active in the larva undergo degeneration, like the rest of the larval tissues, whilst those which are embryonic in type undergo evolution during the formation of the nymph.

As the embryonic portion predominates over the active nervous elements, I propose to speak of the whole as the 'neuroblast,' as a more appropriate term than 'central nervous system of the larva,' although the latter forms a portion which is easily recognised, but cannot be very definitely limited, except by a most detailed and elaborate description.

The **Neuroblast** is formed by the fusion of the primitive ganglia of the embryo; these undergo partial differentiation into nerve-cells and stroma, and remain more or less separated by mesoblastic tissue, so that tracheal vessels are found in the substance of the organ. A large part of the cephalo-thoracic ganglia remains embryonic, whilst a smaller portion of the abdominal, and that only in the more anterior ganglia, retains embryonic characters.

I am not aware that any close investigation of this remarkable organ has been made by any previous writer, and with the exception of a description of the manner in which the optic lobes of the imago are evolved, by Viallanes, to which I shall have occasion to refer subsequently, I have been unable to find any more detailed description than that which Weismann published in 1864. He says:

'The central portion of the nervous system of the larva differs remarkably from that of other insects, inasmuch as there is no ventral cord, but a conical nerve mass, the virtual construction of which, from the ganglionated cord, is not betrayed even by a vestige of lateral constrictions.

'The infra-œsophageal ganglia are intimately fused with those of the thorax and abdomen, whilst the pre-oral ganglia assume the form of "hemispheres," are nearly spherical, and are united with the ventral cone by short thick crura, leaving only a narrow space between them for the passage of the œsophagus. The "hemispheres" lie on the dorsal aspect of the ventral cone, so that seen in profile the whole resembles the butt-end of a pistol.

'The central nerve-mass is about one-twentieth of the body length—in a

larva 1·5 centimètres long, it only measures ·74 to ·78 mm. All the nerves originate from the ventral cone, and there are twelve pairs, two from the front and ten from the sides.'

In this statement Weismann evidently made a slight error, as he subsequently describes the origin of the optic nerves from the hemispheres; moreover, a pair of antennal nerves arise from them: both these are, however, remarkable, as they are the nerve-stalks of the antennal and optic discs and although undoubtedly nerves, inasmuch as they contain nerve fibres, they consist, like all the nerve-stalks of the imaginal discs, principally of embryonic tissue.

Weismann continues: 'The hemispheres and ventral cone consist of a thin, tough external capsule and its cellular contents; the cells are like the nerve cells of most insects: small and spherical and without visible processes; they lie close together, and are arranged in no definite order.'

In these statements Weismann was only correct in part, the cells he saw were the embryonal elements, and he had not the means at his disposal—the preparation of thin sections—which would have enabled him to arrive at more correct conclusions.

He further states that 'the nerve centre exhibits a clear cortex and a dark medulla, and is one of the few examples of a tissue permeated by tracheal vessels. In each hemisphere a tracheal trunk passes, without dividing, almost into the centre of the organ, and then gives off a number of fine radial branches. In the ventral cone the greater part of the tracheal net lies on the surface, only in the middle line of the dorsal region a few air-vessels pass into its substance; these perforate the nerve-mass in a vertical direction and give off branches in a stellate manner to a limited region in its substance.'

I shall not give a very detailed account of the neuroblast in this section, as it will be more convenient to do so after describing the central nervous system of the imago, in the section devoted to its development, but shall content myself by describing its most salient features.

The **Capsule** consists of a thick layer of mesoblast formed of a reticulum of stellate cells, and is richly supplied with tracheal vessels. It not only covers the surface of the neuroblast, but dips in between its constituent ganglia (Pl. III., *cc*), more especially in the median line and around the base of the hemispheres—an arrangement which accounts for the penetration of the tracheal vessels into the interior of the neuroblast.

The **Cortical Substance** consists in great part of embryonic cells, but stellate and fusiform cells are found in great numbers in the immediate vicinity of the nerve-roots around the œsophagus, and on the dorsal surface of the abdomino-thoracic

ganglia; indeed, towards the posterior extremity of the organ they appear to replace the embryonic elements entirely.

Some of these cells attain very large dimensions, especially in the hemispheres close to the œsophagus (Pl. II., Fig. 3, *sc*); similar cells are also found in the same region in the imago.

The central substance, Weismann's medulla, consists of non-medullated stroma; it is divided into two lateral halves, united by a transverse commissure (Pl. III., Fig. 1), and exhibits several distinct tracts.

In the newly-hatched larva the neuroblast is proportionately much longer than in the adult, and exhibits a distinct division of the pro-cephalic portion of the central stroma into three masses (Pl. II., Fig. 7), which correspond with the proto-, deuto-, and trito- cerebrum of Viallanes, and develop into the cerebrum and corpora fungiformia, the corpus centrale, and the olfactory (antennal) ganglia respectively. In the adult larva the ventral portion of the central substance exhibits a large number of distinct bundles of vertical fibres on either side, but contiguous to the middle line.

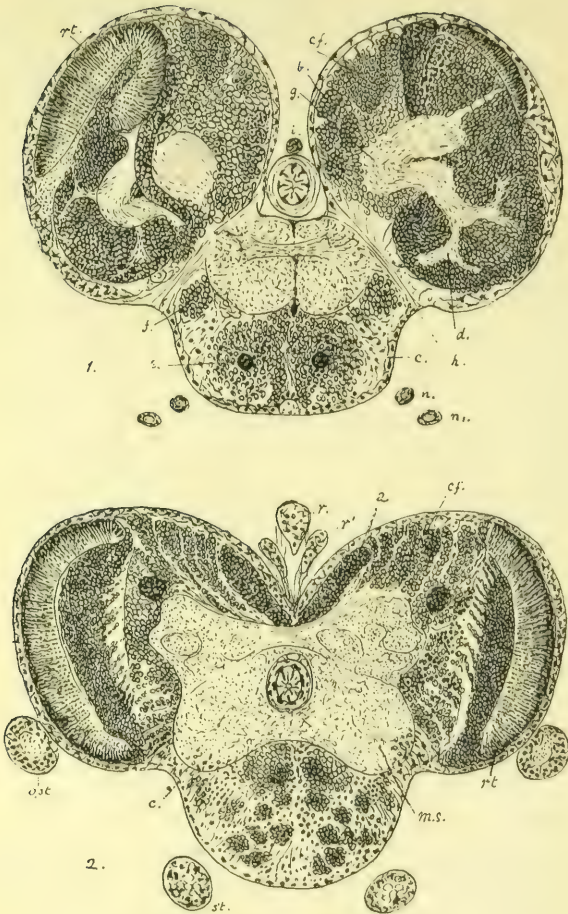
The hemispheres are connected with the post-oral or infra-œsophageal portion of the neuroblast by a pair of thick crura (Pl. III., *m s*), and with each other, above by the supra-œsophageal commissure, and below by the conjoined antennal and infra-œsophageal ganglia.

The rudiments of the corpora fungiformia (*cf*), and of the cerebrum and optic ganglia, of the imago, can be distinctly recognised (*d*); but the most remarkable structure is a layer of infolded epiblast (*rt*), from which the retina is subsequently formed in the nymph. This is an imaginal disc, which lies within the capsule of the neuroblast, whilst the eye-disc of Weismann, from which the rest of the eye is formed, lies out-

PLATE III.—TRANSVERSE SECTIONS THROUGH THE NEUROBLAST OF THE ADULT LARVA.

FIG. 1.—Through the Posterior Part; and FIG. 2.—Through the Centre of the Hemispheres. *a, b*, and *cf*, Parts of the corpus fungiforme; *d*, the trabecula and its divisions; *r r'*, the ring; *rt*, retina; *c*, capsule; *s, f*, nuclei of infra-œsophageal ganglia; *m s*, stroma; *o st*, optic stalk; *st*, stalk of inferior mesothoracic disc; *z*, median stomogastric nerve.

PLATE III.



THE NERVOUS SYSTEM OF THE ADULT LARVA.



side the capsule of the neuroblast, with which it is connected by the optic stem.

The antennal ganglia (Pl. III., Fig. 2) exhibit a peculiar grouping of cells in small spherical masses, imbedded in a reticular substance. The infra-oesophageal ganglia have a similar structure, but each has a single large group of cells arranged in concentric layers (Pl. III., Fig. 1, *s*) with smaller lateral groups (*f*) scattered through the reticular substance.

The description of the splanchnic nervous system will be more conveniently given after I have described the remaining structures of the larva.

### 8. THE SENSORY ORGANS AND PERIPHERAL NERVE TERMINATIONS.

With the exception of the sensory papillæ, described on p. 36, the only special sensory structures I have been able to



FIG. 12.—1. A section of the terminal joint of the Maxilla, showing the eye-like organs; 2. A section of the eye-like organ ( $\times$  oil immersion lens); 3. Endings of a nerve in the hypodermis, showing a peripheral ganglion ('à côtes de melon,' Viallanes).

discover are the pair of eye-like organs at the extremity of each maxilla. Newport recognised the existence of similar struc-

tures in the larva of *Æstrus*, and suggested that they are probably eyes. That the larva of the Blow-fly is extremely sensitive to light is certain.

These eye-like organs (Fig. 12, 1 and 2) resemble the simple eyes of the leech, but are devoid of pigment. The two in each maxilla are situated on branches of the same nerve, each is surrounded by a delicate reticular capsule, and is capable of retraction. The epiostracum forms a thin, transparent cap over the surface of the nerve terminals, which are long rod-like cells, with a distinct layer of stellate and fusiform ganglion cells between them and the nerve.

The majority of the cutaneous nerves apparently end in the cells of the hypodermis (Fig. 12, 3) in demilunes of granular protoplasm (see Histology), and many of these exhibit a remarkable form of peripheral ganglion, first described by Viallanes, and called by him 'Ganglion à côtes de melon.' The ganglia are small groups of unipolar cells attached to the sides of the nerves. The cells present a striking analogy with those of the root ganglia of the spinal nerves of vertebrates.

## 9. THE IMAGINAL DISCS.

### a. General Morphology.

The Imaginal discs have been already referred to (pp. 3 and 21) as the structures from which the nymph is developed.

#### Bibliography :—

31. LACHÂT ET AUDOUIN, 'Anatomie d'une larve apode trouvée dans le Bourdon des Pierres.' *Journ. de Physique, de Chimie, etc.* Tom. lxxxviii., p. 228, 1819.
32. DUFOUR, LEON, 'Études Anatomiques et Physiologiques sur une Mouche.' *Mém. Pres. à l'Acad. des Sc., Math. et Phys.* Tom. ix., 1846.
33. WEISMANN, A., 'Die Metamorphose der *Corethra plumicornis*.' *Zeitsch. f. w. Zool.*, Bd. xvi., 1866.
34. GANIN, M., 'The Post-Embryonic Development of Insects.' In Russian. Transactions of the 5th Congress of Russian Naturalists. Warsaw (1875), 1876. (*S'yezd Russkikh Estestvoispytatelei Trudui v. Varshavye.*) Résumé in German, *Zeitsch. f. w. Zool.*, Bd. xxviii., pp. 386-389, 1877; and *Jahrb. d. Anat. u. Phy.*, Bd. v., p. 507, 1878.
35. DEWITZ, 'Beiträge zur Kenntniss der Postembryonalen Entwicklung der Gliedmassen bei den Insekten.' *Zeitsch. f. w. Zool.*, Bd. xxx., Suppl., 1878.

These exist in the larva as encapsulated groups of embryonal cells, and vary greatly in form; for the several discs not only differ from each other, but exhibit considerable variations at different stages of development. Many are capable of easy demonstration in the adult or even in the young larva; whilst others do not become apparent until the nymph is partially developed. As all the discs preserve an embryonic character, it is probable they are all present in the young larva, or even in the embryo, as distinct groups of cells, but only the larger ones have been actually demonstrated at the earlier periods of development; and it is only in the later stages that the smaller discs can be safely recognised.

**History.**—The larger discs in the larva of the Muscidæ were first seen by Swammerdam [4], who, from their relation with the nerve-centres, mistook them for ganglia. Lachât and Audouin [31] termed them '*Plaques*'; Leon Dufour [32], '*Corps ganglionöides*'; and Leuckart [20] and Scheiber [21] described them as ganglia. Weismann [2] discovered their true nature, and named them '*Imaginal Scheiben*,' of which the English equivalent, Imaginal discs, is generally accepted. Ganin [34], in a paper in Russian, added much to our knowledge; but, unfortunately, Ganin's work is only accessible to me by short translations of certain portions of it [27, 34].

**Morphology.**—The view of the nature of the discs which I have adopted (p. 21), although supported by the researches of Dewitz [35], Künckel d'Herculais [25], and others, is at variance with the views of Weismann [2] and Ganin [25, 27, 34]. Both these distinguished naturalists examined the structure of the thoracic discs with great care, at the earliest stage of development in which they are recognisable, and concluded that they originate from the nerve-sheaths and the peritoneal tissue of the tracheæ to which they are attached.

It must be confessed that in the earlier stages of development, appearances favour the views of Weismann and Ganin; on the other hand, the hypothesis which derives epiblastic structures from the mesoblastic connective tissues, and severs the development of the Muscidæ from all other insects, is one

which possesses such inherent improbability, that even if there were no observations in support of more probable views, one would have been tempted to doubt the conclusions on which it rests, even although the facts observed are substantially as stated by Weismann and Ganin.

The most rudimentary discs (Fig. 3, 1) do not appear very distinctly until the pupa stage; they are mere groups of embryonic cells, which project on the surface of the hypodermis, and are the rudiments of the abdominal somites. In some sections of larvæ I have detected small groups of embryonic cells in the same position; and, from the characters of the discs, I think it probable that they are derived directly from epiblast cells.

Ganin says 'the transformation of the great polygonal cells of the larval hypoderm into small embryonic cells commences at four points in the lateral regions of the segments, and the new formation is preceded by a separation of the hypoderm and muscles of the larva and its cuticle.' He adds, 'these cells arise from the old cells of the larval hypoderm.' These extracts are quoted by Viallanes [27, p. 215], who remarks that, 'The replacement of the larval by the imaginal hypodermis is analogous to that of the milk by the permanent teeth in mammals. In the insect four germs exist in each somite, which at a certain period undergo evolution, and determine the shedding of the hypodermis of the larva.'

Viallanes appears to me, in this and the following statements, to have correctly appreciated the true morphological character of the imaginal discs. He says:

'The facts observed by Weismann in *Corethra*, and those discovered by Künckel in *Volucella*, must lead us to believe that the discs are derived from the hypoderm [or epiblast].\* In insects we [frequently] observe that the imaginal discs are united with the hypoderm, either directly, or by a more or less elongated pedicel. The variations which are observed in different species, or in the same species in different parts,

\* The words in brackets are added by me, and, with their addition, I entirely agree with Viallanes.

appear to depend on the period at which the discs are first developed.

'In the abdominal region of the fly the discs first appear at the end of the larval period, so that their evolution follows immediately; thus they remain superficial. In the thorax of *Corethra*—Weismann—and of *Volucella*—Künckel—the discs are formed at the commencement of larval life, and become invaginated, only retaining their union with the integument by a [hollow] pedicel of variable length. In the thorax of the fly they are formed much earlier; they already exist in the embryo in the egg. It is perhaps on this account that there is no apparent connection with the integument; but further researches on this point are needed.

'It is, perhaps, important to observe that this peculiar method of development is not confined to the Insecta. The researches of Barrois have established the fact that in *Pilidium*, amongst the Nemertids, the phenomena observed are similar, since in these worms the larval exoderm is shed and is replaced by one developed from germs analogous to imaginal discs; and the analogy is rendered the more striking, as in the different species of Nemertid the same differences are met with as in insects exhibiting a higher or lower degree of metamorphosis' [27, p. 224].

My own researches show that in the adult larva of the Blowfly there is precisely the same connection between the epiblast of the disc and the hypoderm as that which has been observed in the ant (*Dewitz* [35]), and in *Corethra* [33] and *Volucella* [25] (Fig. 15, 2). Moreover, in the maxillary discs and those of the anterior spiracle the sac is still a wide open ampulla, and the invagination of the frontal lobes has been already referred to (p. 42). I attribute the failure on the part of Weismann and Ganin to trace the connection as due to the difficulties which attend the investigation in young larvæ.

In the advanced types of disc, such as the leg discs of the fly (Fig. 15), the invaginated hypoderm exhibits a distinct differentiation into two parts, a disc sac, *s*, the provisional capsule of Ganin, and the epiblast of the disc. The latter

consists of one or more layers of cells, those on the surface, which is enclosed by the provisional capsule, are distinctly columnar, those beneath, nearer the mesoblastic surface, are small round or fusiform cells. The mesoblastic surface is usually concave, and its cavity is occupied by a layer of stellate mesoblast.

The great discs of the head and the inferior pro- and mesothoracic discs are so intimately connected with the neuroblast by neural stalks, and are apparently so far removed from the hypodermis, that it is not difficult to understand how Weismann and Ganin arrived at the conclusion that they originate from the sheaths of the nerves.

The rudiments of these discs certainly appear in the embryo, close to the roots of the nerves to which they become adherent, whilst the nerve-centres are in contact with the ventral integument: as the growth of the larva is rapid whilst that of the neuroblast and discs is slow, the latter soon become separated from the hypodermis; and the pouches which contain the rudiments of the discs are drawn from their points of origin, leaving the neck of the disc-sac as a very narrow tube attached to the growing peripheral portion of the corresponding nerve. The neck of the sac is not readily seen, hence Weismann regarded the bands which he saw in the adult larva connecting the discs with the integument as nerves or of secondary import.

The portion of the nerve between the disc and the neuroblast becomes greatly enlarged towards the end of larval life, owing to the rapid multiplication of the mesoblastic elements of its sheath, which are continuous with the mesoblast of the disc.

The epiblast of the disc, as development progresses, usually becomes much folded or invaginated into itself; its cells are then found united by an intercellular substance resembling chitin, and one or more thin layers of cuticle are often shed from its surface. The disc-sac or provisional layer of Ganin consists of thin tessellated cells, or may exhibit transitional characters both at the edge of the disc and in the vicinity of

the hypodermis. In the later stages it becomes so thin that its original cellular character can no longer be recognised.

The **Mesoblast of the Disc** was first discovered by Ganin; it consists of a stroma of stellate cells, permeated by fusiform cells, tracheæ, and nerve-fibres. It frequently covers the whole outer surface of the provisional sac, but is thickest in the hollow of the disc itself, in which a cavity is usually present, which communicates with the body cavity of the larva, and, like the latter, is filled with blood.

The origin of the mesoblast of the disc, like that of the mesoblast of the embryo, is unknown. Künckel d'Herculais [25] supposed it to be developed from peritracheal cells, or from the leucocytes of the larva, but left these alternatives unsupported by facts. Its continuity with the tissue of the nerve and tracheal sheaths is perhaps in favour of the former view; but it is equally probable, I think, that it is developed by differentiation from the disc itself. This much is certain, it cannot be demonstrated in the earlier stages of disc development.

#### b. The Cephalo-Thoracic Discs.

The cephalo-thoracic discs may be studied in the larva; the abdominal discs are more readily demonstrated during the earlier stages of the development of the nymph.

There are nine pairs of discs concerned in the development of the head and thorax. The great cephalic discs, and the maxillary and labial discs, form the head and proboscis, an upper and a lower pro-, meso- and metathoracic disc on each side unite to form the thorax.

The **Great Cephalic Discs** (Pl. IV., *op d*, *an d*, and *pc d*, and Fig. 13) are formed, as already indicated, by an invagination of the frontal lobes of the embryo (Fig. 7).<sup>\*</sup> They extend from the posterior extremity of the cephalo-pharynx to the anterior portion of the neuroblast, and are suspended by the cephalo-pharyngeal band and the ring (Fig. 13, *cp*, and Fig. 14, *r*). The manner in which they are disposed will be understood by a

<sup>\*</sup> Weismann [33] has figured a similar condition in *Chironomus*; compare his Figs. 17 and 25 with my Fig. 7.

reference to Fig. 14, 2, which represents a transverse section through the region indicated by the line 2 in Fig. 13: *cp* is the cephalo-pharyngeal band; *sp*, the suspensory membrane, and *a*, the base of the antennal rudiment.

There is a large blood sinus between them, in which the cesophagus lies, into which the dorsal vessel opens through the ring. The suspensory membrane, *sp*, forms its roof, and the

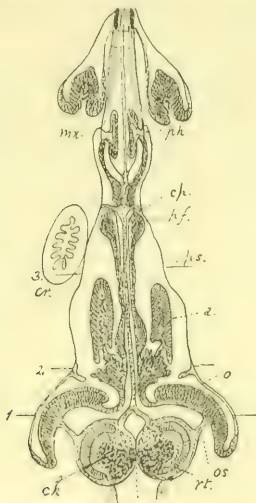


FIG. 13.—A semi-diagrammatic representation of the Head Discs and Hemispheres seen from above: 1 2 and 3, planes of the sections 1 2 and 3 in Fig. 14; *mx*, maxillary disc; *ph*, pharyngeal; *a*, antennal; *o*, optic discs; *pf*, prefacial rudiment; *cp*, cephalo-pharyngeal band; *cr*, crop; *ch*, cerebral hemisphere; *rt*, retina; *os*, optic stalk; *ps*, provisional sac.

discs its lateral walls. The inner and posterior part of the wall of the disc sac is occupied by the epiblast of the disc; its outer wall is the provisional membrane.

The Ring was first described by Weismann as follows [2, p. 125]: 'The anterior part of the dorsal vessel lies above the

nerve-centres, and passes between the hemispheres; immediately in front of these there is a ring of cellular tissue, with a lumen large enough to transmit the vessel. The ring hangs freely in the body cavity, and is fixed by fine tracheal vessels.

‘In the anterior part of the second segment’ (my fourth somite) ‘a tracheal branch arises from the main trunk, passes inwards and backwards, and ultimately penetrates the hemisphere. In its course this trachea is united to its fellow by a transverse vessel which lies in the upper’ (anterior) ‘part of the ring; whilst the trachea courses through the side and back part of the ring. The peritoneal coat of these vessels is fused with the tissue of the ring, so that the latter might perhaps be regarded as a development of the peritoneal layer of the tracheæ. This is, however, not so; the tracheæ have little to do with the formation of the ring, as this is clearly an organ which originates in the embryo; its form is that of a simple broad finger-ring, the upper segment somewhat notched in the middle line. The diameter of the ring is about .23 mm., measured from before backwards; the dorsal vessel is attached to it, dilates in front like a funnel, and is finally attached to the pharynx.

‘There can be no doubt the ring is a skeletal structure, and in this relation I have not fully described it, for it gives off an anterior and a posterior band.’ At this point Weismann’s description becomes so complex that I shall only give a *résumé* of his meaning as I understand it. The anterior band connects the anterior (upper) part of the ring with the cornua of the cephalo-pharynx—this is my cephalo-pharyngeal band; the posterior band is continued over the œsophagus and terminates in a transverse enlargement in front of the proventriculus, to which it is firmly attached. This posterior band is undoubtedly the stomogastric nerve, which is connected through the frontal ganglion with the crura of the hemispheres and the dorsal vessel by numerous nerve-fibres, which lie upon the surface of the ring, and which were overlooked by Weismann.

I have not the slightest doubt the cephalo-pharyngeal band is the remains of the invagination of the procephalic

lobes; and that the ring is an indication of its origin from two lateral halves. The band and ring consist in the adult larva of a solid epithelial tissue, in which the intercellular substance is much developed; it is exceedingly like cartilage, and closely resembles the endo-thoracic skeleton of the scorpion described by Prof. R. Lankester.\* The changes which the ring undergoes in the later stages of the larva are very marked; in the feeding larva it is nearly vertical, and the nervous elements on its exterior are very distinct; in the resting larva it grows rapidly and becomes nearly horizontal, so that its upper border becomes anterior and its lower border posterior. The nerve elements are then inconspicuous in relation to the skeletal quasi-cartilaginous substance of the ring itself.

The ring and cephalo-pharyngeal band support the great cephalic disc sacs, the provisional membranes of which are continuous with its edges (Fig. 14, *sp*).

The disc sac is differentiated into the optic, antennal, pre-facial and pharyngeal rudiments (Fig. 13).

**The Optic Rudiments or Discs** are cup-shaped in the feeding larva, and lie in front of and above the hemispheres, with which they are connected by the optic stalks. As development progresses, their outer and inferior borders become greatly thickened and folded, so that they are sub-triangular when seen in profile (Plate IV.).

Weismann compared the optic disc to a mushroom with an excentric stalk, the optic stalk. The latter is solid at first, but a canal is afterwards formed in its interior, through which the retinal disc ultimately reaches the inner mesoblastic surface of the optic disc. I shall show hereafter that the optic disc is concerned in the development of the dioptric structures of

\* 'On the skeleto-trophic tissues and coxal glands of *Limulus*, *Scorpio* and *Mygale*.' Quart. Journ. Micros. Sc., vol. xxiv., new series, 1884.

PLATE IV.—THE NEUROBLAST AND THE IMAGINAL DISCS CONNECTED WITH IT  
IN THE RESTING LARVA.

*r*, The ring; *d v*, dorsal vessel; *a*, the cesophagus; *op d*, optic disc; *an d*, antennal disc; *pc d*, prefacial rudiment and pharyngeal disc; *ph*, cephalo-pharynx; *tr*, trachea; *bt d*, prothoracic leg disc; *mt d*, mesothoracic leg discs; *n*, nerve.

PLATE IV.



THE IMAGINAL DISCS OF THE RESTING LARVA, FIRST STAGE.



the compound eye (the Dioptron, *Mili*), whilst the retinal end organs originate from the retinal disc (Fig. 13, *rt*). This, which I have not included amongst the head discs, is formed

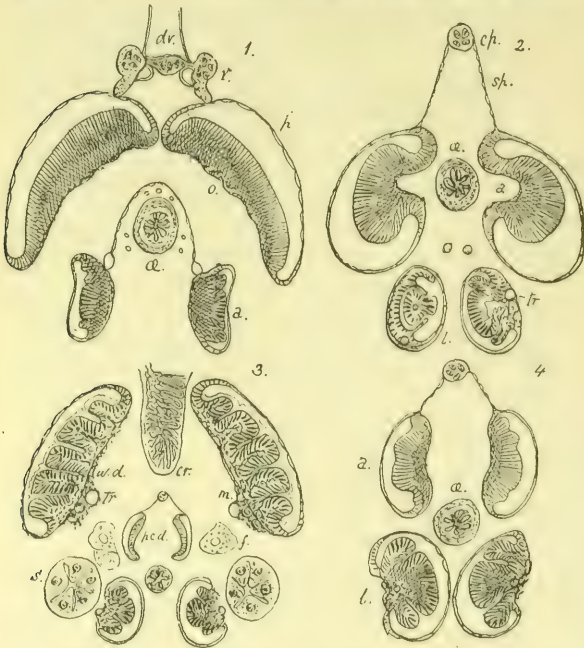


FIG. 14.—Transverse Sections through the head discs (see Fig. 13): *dv*, dorsal vessel; *r*, ring; *p*, provisional sac; *o*, optic; *a*, antennal; *l*, leg; *wd*, wing discs; *a*, oesophagus; *s*, lingual gland; *pcd*, prefacial rudiment; *f*, fat cell; *tr*, trachea; *sh*, suspensory membrane; *ch*, cephalo-pharyngeal band.

on the outer surface of the neuroblast, and is entirely enclosed in its capsule. In its relation with the nerve-centre it presents a striking analogy with the primary optic vesicle of a vertebrate.

The Optic Stalk (Pl. III., *o st*, Pl. IV., and Fig. 13, *o s*)

consists of a thick, hollow, neural sheath of stellate mesoblastic cells, enclosing a few nerve fibres. It arises from the upper and outer part of the hemisphere in the young larva, but as development progresses, owing to the great enlargement of the hemisphere, it is gradually pushed downwards and outwards, so that it finally arises from the lower and posterior portion. The nerve-fibres of the optic stalk traverse the mesoblast of the optic disc, and form a small nerve, which passes forward by the side of the pharynx and œsophagus, and probably supplies the simple eyes at the extremity of the maxilla. I cannot be certain of this, however, as I have been unable to trace the entire course of this nerve.

Each lateral half of the frontal region is developed from the epiblast of the posterior part of the inner wall of the disc sac, which is connected with the lower border of the optic disc behind, and supports the antennal rudiment in front. The antenna originates from a central papilla, surrounded by two concentric rings. The central papilla becomes the third antennal joint. In front of the antenna a thin band of epiblast is continued forwards; it terminates in a bulb-like prefacial enlargement, and sends a process into the cephalopharynx, between the cornu and the inferior process, the rudiment of one lateral half of the fulcrum of the imago.

Menzbier\* and Künckel d'Herculais [25] regarded the optic discs and the antennal and prefacial rudiments as distinct, and have deduced theoretical conclusions on the segmentation of the head from this assumption. There is a distinct continuity of the epiblast, and the whole are enclosed in a single disc sac. I am unable, therefore, to admit the validity of such conclusions.

**The Appendicular Discs of the Head.** The maxillary discs (Fig. 13, *mx*, and Fig. 8, *2*) first appear late in larval life as invaginations of the hypoderm of the stomal disc. One appears close to the outside of the attachment of the great hook on each side. The labial discs are represented in the adult larva by a small group of cells on either side of the lingual (salivary) duct near its orifice.

\* 'Über das Kopfskelet u. s. der Zweiflügler.' Bull. Soc. Imp. Nat., Moscou, tom. lv., 1880.

Künckel d'Herculais [25] figured and described three pairs of appendicular discs in the resting larva of *Volucella*—a pair of mandibular, a pair of maxillary, and a pair of labial discs. The two latter correspond with those of the Blow-fly larva, but I have been unable to find any traces of mandibular discs. Weismann knew nothing of the appendicular head discs.

The **Thoracic Discs** are arranged in two groups. Four neural discs attached to the second and third pairs of nerves lie beneath the neuroblast and the great cephalic discs. These are the inferior, pro- and mesothoracic discs. Four pairs are closely related to the great tracheal trunks, the upper pro-, meso- and metathoracic, and the inferior metathoracic discs (Fig. 16).

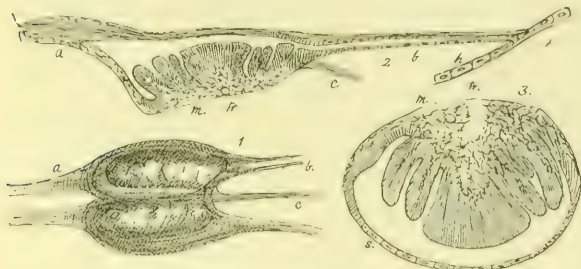


FIG. 15.—Leg Discs: 1, the prothoracic leg disc from the adult larva; 2, longitudinal section of, the mesothoracic leg disc of the same; 3, transverse section of the same; *a*, neural stalk; *b*, neck of sac; *c*, nerve after traversing mesoblast of the disc; *m*, mesoblast; *s*, sac of disc; *h*, hypoderm; *tr*, tracheæ.

The inferior thoracic discs may be called for brevity leg discs. The prothoracic pair are enclosed in a single sac, and are connected with the hypodermis by two distinct necks (Fig. 15, 1 *b*), and with the neuroblast by a pair of nerves.

The mesothoracic leg discs are not united; they lie below and a little behind the prothoracic discs.

The concentric structure which the leg discs exhibit in optical section is due to the arrangement of the epiblast (Fig. 15). The central papilla is the rudiment of the last tarsal joint, and

the ridges which surround it become the other tarsal joints, except the outermost, which is the rudiment of the femoro-tibial part of the leg. The most external portion of the epiblast becomes the sternal region of the thorax.

The leg discs, in an early stage of development, exhibit only the central papillæ, and the number of concentric rings increases as development progresses.

The superior prothoracic disc (Fig. 11, 3) is formed by an involution of the hypoblast at the base of the anterior spiracle; it appears first towards the end of larval life, and, according to Weismann, it is the only thoracic disc not present in the

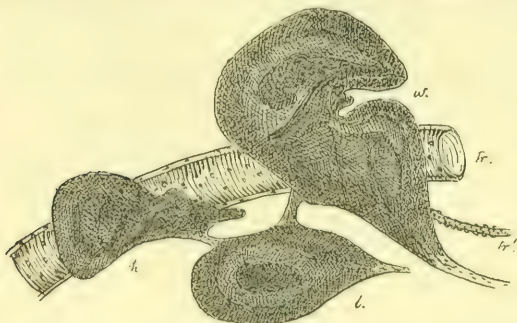


FIG. 16.—Group of tracheal discs from an adult larva: *w.*, wing disc; *h.*, superior, and *l.*, inferior metathoracic discs; *tr.*, main trachea; *tr.*, modified tracheal vessel, seen with an inch-objective.

young larva. At the end of the resting stage, or early in the pupa stage, the mesoblast of this disc surrounds the main tracheal trunk, and unites it with the mesoblast of the superior mesothoracic disc.

The superior mesothoracic, or wing, disc (Figs. 14, 3, and 16) lies above and in front of the great cephalic disc. It is the largest of all the imaginal discs. Its epiblast is corrugated, so that it presents numerous concentric lines when seen in optical section. The wing projects from the surface of the disc as a conical papilla.

The superior metathoracic disc is placed behind and below the superior mesothoracic disc. It is exceedingly like the latter, but much smaller. It is attached by bands of mesoblast to the wing disc, and to the metathoracic leg disc. One or more of the tracheæ which are in relation with the wing disc are usually entirely surrounded by minute embryonic cells, which are probably the rudiments from which the wing tracheæ of the nymph are developed (Fig. 16, *tr'*). Similarly modified tracheæ are also found in relation with the other discs in the resting stage of the larva.

#### 10. THE CŒLOM, DORSAL VESSEL, AND SPLANCHNIC SYSTEM OF NERVES.

**The Cœlom.**—By the term cœlom, I include all the tissue interspaces between the hypodermis and the viscera. It contains a reticulum of cells, which divides it into larger and smaller blood sinuses. The cells may be classed in the following groups: endothelioid, stellate, connective, adenoid, and fat cells; but numerous transitional forms occur, and the whole are probably modifications of the primary stellate mesoblast.

Under the term endothelioid, I include the cells of the sub-hypodermic layer, those of the peritoneal coats of the tracheæ and viscera, and true endothelial plates which bound the larger blood sinuses. They pass by numerous transitional forms into the stellate connective cells, in which the tracheal capillaries are developed.

Under the term adenoid, I include certain strings of cuboid or spheroidal cells, which often attain a large size, and are frequently multi-nucleated; sometimes as many as four or five nuclei are present in each cell. They form Weismann's cell-chaplet (see page 61), the pericardial septum, and the fringes of the dorsal vessel.

The fat cells are also united in strings, and form a large reticular sheet, the fat body or omentum. This appears to the naked eye as a glistening, opaque, white sheet of tissue, which floats out of the body cavity when the integument is slit up

under water. It consists of a median dorsal and two lateral lobes. Sections show that the omentum is much folded and convoluted, that it occupies the greater part of the body-cavity, and has large blood sinuses between its folds.

The cells of the fat body (Fig. 19, *f b*) measure about 0.15 mm. in diameter; they consist of a reticular protoplasm, in the meshes of which granules and globules of fat are imbedded. These are so numerous that they conceal the nucleus. Sections show that the cells are bounded by a thin cuticular membrane. These cells have large vesicular nuclei, which undergo very remarkable changes during the development of the nymph.

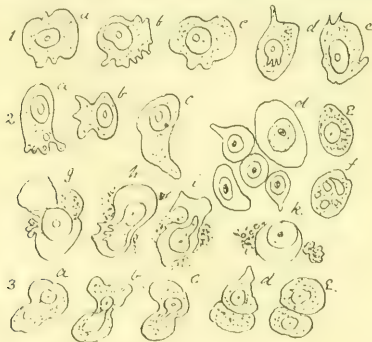


FIG. 17.—Blood corpuscles (*leucocytes*) of the adult larva: 1, living corpuscles, showing the amoeboid condition, in *d* the nucleus is also amoeboid; 2, the same, treated with magenta, showing the various appearances produced by the action of the reagent; 3, a living cell in several stages of direct division, all drawn with  $\frac{1}{17}$  oil immersion lens. (For details see 'Histology of Tissues'.)

The fat body, although adherent in places to the larger tracheal vessels, has no tracheal capillaries developed on its surface. When removed from the larva and exposed to the air, it rapidly assumes an inky hue, probably the result of oxidation. The contents of the cells are not easily acted upon by osmic acid, unless the outer wall of the cell is ruptured.

The cells of the fat bodies increase rapidly in size with the growth of the larva, and, except in very young larvæ, do not appear to increase in number.

The fat body is undoubtedly the principal store of nutrient material for the development of the imago.

**The Blood** of the larva consists of an opalescent spontaneously coagulable fluid, and has a large number of amœboid corpuscles  $5\mu$  to  $6\mu$  in diameter (Fig. 17). It permeates all the tissue spaces of the cœlom, but there are several distinct blood sinuses through which the direction of the blood stream appears to be constant. The largest are the great ventral and the pericardial sinuses.

**The Great Ventral Sinus** commences between the imaginal discs of the head, and extends forwards to the pharynx and maxillæ as the cephalo-pharyngeal sinus, and backwards surrounding the neuroblast and the alimentary canal as far as the posterior border of the 12th somite, where it is lost in spongy tissue, through which the blood ascends to the pericardial sinus.

**The Dorsal Vessel** (Figs. 18 and 19). There is no organ in the larva the study of which presents such difficulties as the dorsal vessel. It is a muscular tube which extends from the posterior transverse tracheal trunk to the ring, to both of which it is attached. As Weismann pointed out [2, p. 121], it consists of three parts, which I shall distinguish as the ventricle, the intermediary portion, and the aorta.

**The Ventricle** (Fig. 10, *dv*) is ovoid, flattened from above downwards and constricted at two points, so that it consists of three chambers. It lies in the dorsal or pericardial sinus, and is separated from the intestines by a partial septum—the pericardial septum.

**The Pericardial Sinus** lies immediately beneath the dorsal integument of the 11th, 12th, 13th, and 14th somites. The ventricle only partially fills the cavity, which contains tufts of fine tracheæ and a quantity of lymphoid tissue, indistinguishable from the lymphoid tissue of vertebrates. This is especially abundant on either side of the ventricle.

Viallanes [27, p. 66] describes the dorsal vessel of a young dipterous larva, which he refers to the genus *Ctenophora*, in which he observed tufts of fine tracheæ in the pericardium, and the connection of the dorsal vessel with the transverse anastomotic tracheal trunk. He adds :

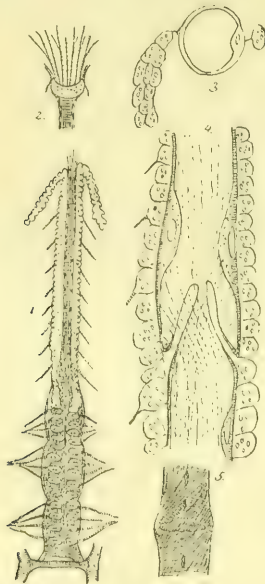


FIG. 18.—The dorsal vessel : 1, a semi-diagrammatic representation of the two posterior sections, showing the large cells of the pericardial septum, the alæ musculares and the cell fringes ; 2, the anterior extremity of the aorta and the ring ; 3, a transverse section of the intermediary portion ; 4, a longitudinal section of the same, with a pair of valves, seen from above, showing the internal cells, cell fringes and alæ musculares ; 5, a lateral view of a valve pouch— $\frac{1}{2}$  oil immersion lens.

‘It appears, therefore, that in this larva the dorsal vessel is an arterial heart, since the blood which enters it has passed

through the floating branches of a rich tracheal arborescence. Thus the respiratory function appears to be localized in the last segment, and there are few tracheæ in other regions of the body.'

The paucity of tracheæ in the young larva of the Blow-fly was observed by Weismann, but in the adult larva they are



FIG. 19.—Sections through the pericardial sinus, with the dorsal vessel in situ: 1, near the anterior, and 2, near the posterior extremity of the ventricle; *p s*, pericardial sinus; *f b*, cells of fat body; *a m*, alæ musculares; *i s*, ventral valve; *m*, dorsal recti muscles; *i*, intestine; *p c*, cells of the pericardial septum; *tr*, trachea.

abundant, a fact which does not, however, render the presence of numerous tracheæ in the pericardial sinus less interesting.

**The Pericardial Septum** (Figs. 18 and 19) forms the floor of the pericardial sinus. It consists of a double row of large ovoid cells.

Weismann [2] states that there are thirteen on each side of

the middle line, but I have been unable to determine their number, which appears to me variable. These cells are oval in transverse section and measure  $\cdot 1$  mm. in long diameter; they stain deeply and have large oval nuclei. They are connected with the muscular alæ of the ventricle, and I have frequently traced a direct continuity of their cell substance with a muscle fibre.

**The Muscular Alæ of the Ventricle** consist of three groups of diverging muscle fibres on each side (Fig. 18, 1), which are inserted in part into the cells of the septum and in part into the middle line of the ventral surface of the ventricle. The finest of these fibres are not more than  $2\mu$  to  $3\mu$  in diameter, and are very distinctly striated. They are surrounded by a myolemma, which also encloses the large cells of the septum.

The muscular alæ appear to arise from the peritoneal coat of the great lateral tracheal trunks, and they divide and subdivide in their course towards their insertion.

**Valves.**—The cavity of the ventricle communicates with the pericardial sinus by a series of slit-like openings, guarded by valves. It is exceedingly difficult to determine the exact number of these openings, as they are most readily studied in transverse sections. There are certainly two lateral openings to each chamber, and one or more ventral slits.

There are also several openings (four?) at the posterior extremity of the heart.

The ventral openings (Fig. 19, 2) are between the cells of the septum, and the alar muscles pass into the wall of the ventricle immediately behind them. The valves which guard the openings are thin membranous flaps, which project into the ventricle, and are not nucleated projections of the wall of the cavity. I have been unable to distinguish valves between the chambers of the ventricle.

The second, or intermediary, part of the dorsal vessel (Fig. 18) varies considerably in diameter and in the form of its cross section at different points. It is circular at its origin, becomes pentagonal in the middle of its course, and circular again near its termination. It measures from  $\cdot 15$  mm. to

·25 mm. in diameter, and is smallest at its ends. It dips downwards from its origin, and its termination is near the central axis of the body.

It is not enclosed in a pericardial cavity, but the pericardial septum is continued forwards as a fringe on either side of the vessel, consisting of a double or triple row of cuboid cells. The cell fringes give insertion to small alar muscles at intervals which arise from the lateral tracheal trunks. They terminate in front in Weismann's cell chaplet. When the dorsal vessel is removed from the body the intermediary portion contracts and throws the cell fringes into very regular plications.

The cells which form the fringes and cell chaplet are 25 $\mu$  to 50 $\mu$  in diameter. The marginal cells are cuboidal, and those nearer the dorsal vessel are spheroidal, and usually contain from two to five nuclei.

Similar cell chaplets exist in the imago, and are undoubtedly young fat bodies; and in many insects fat bodies are found attached to the dorsal vessel in the place of cell fringes. I am inclined to regard these structures, therefore, as the young fat cells of the nymph (see Development of the Nymph).

The intermediary portion of the dorsal vessel contains several double valves opening forwards. These are pouches of the lateral walls. The muscle fibrillæ have a somewhat spiral arrangement at the valves, which gives the appearance of a St. Andrew's cross when both sides of the tube are seen superimposed (see Fig. 18, 4 and 5).

The third part of the dorsal vessel, or aorta (Fig. 18, 2), measures about 1 mm. in length. It lies upon the neuroblast and terminates in the ring, from which a number of fine muscle fibrillæ are prolonged forwards, and are attached to the meso-blast of the cephalic discs and to the posterior extremity of the cephalo-pharynx. These fibrillæ lie in the cephalo-pharyngeal blood sinus, and were described by Weismann.

**Structure and Morphology.**—Viallanes [27, p. 58] gave a *résumé* of what was certainly known of the dorsal vessel in 1882, and I do not find that anything has been added to our knowledge since. He said: 'It consists of a tube with two lateral rows

of nuclei in its walls.' He dismissed the researches of Bütschli, Dohrn and Jaworowski in the following words :

' The study of certain embryos leads to the conjecture, which has never been certainly established, that it is formed from a double row of cells, and that each nucleus represents a cell. Thus, it may be said to consist of a series of hollow segments, each formed of two cells, joined in the middle line.'

Viallanes claims to have demonstrated the junctions of the cells by staining the intercellular substance with nitrate of silver, and to have observed muscular fibrillæ, which pass from segment to segment imbedded in the substance of the cells; and he concludes that it is morphologically a capillary blood vessel with muscle fibrillæ imbedded in its cellular walls.

Weismann [2] regarded it as a hollow muscle fibre. I am inclined to consider it a hollow fibre of peculiar construction, and think that its true nature is as well represented by Weismann's as by Viallanes' hypothesis. Its walls are certainly cellular, and consist of muscle fibrillæ, but whether the cells should be regarded as a bed in which the fibrillæ lie or a lining intima having an endothelial character is a point not easily determined. It is certain that a very slight modification of one of the skeletal muscle fibres with central nuclei would render it practically identical with the dorsal vessel if the valves are left out of consideration. As these are, however, a most important element in its construction, it appears to me that Weismann's view is only an approximation to the truth.

The nuclei of the dorsal vessel are arranged with great regularity. They are about  $\cdot 1$  mm. apart, and each measures about  $15^{\mu}$  to  $20^{\mu}$  in diameter. The nuclei are surrounded by more or less granular protoplasm. The muscular layer is external to this cell substance, and consists of fibrillæ  $2^{\mu}$  to  $3^{\mu}$  in diameter. They are chiefly longitudinal in direction. They are most distinctly striated, and the transverse striæ surround the whole tube.

**The Splanchnic Nervous System** consists of a series of visceral ganglia. Those of the pharyngeal sinus, of the crop and

proventriculus are the largest. They are all united with a central ganglion, which I shall term the median ganglion.

The median ganglion is situated on the dorsal surface of the œsophagus, immediately behind the commissure of the hemispheres. It is a pyramidal enlargement of the median splanchnic nerve. It receives several nerve cords from the crura of the hemispheres at its base, and gives off branches from its apex which are attached to the posterior margin and external surface of the ring; they surround the dorsal vessel and supply it, and terminate in the ganglion of the crop.

The portion of the median nerve in front of the central ganglion divides into several branches, which form a plexus around the œsophagus. These end in the ganglion of the pharyngeal sinus.

The **Ganglion of the Pharyngeal Sinus** consists of a number of large stellate nerve cells, the processes of which terminate in the intrinsic muscles of the pharynx. Many of these cells measure 20 $\mu$  to 30 $\mu$  in diameter; they are not closely packed together, but are scattered in the posterior part of the sinus and lie chiefly close to the pharyngeal epithelium. Beside these ganglion cells there is a considerable quantity of lymphoid tissue and a group of cells similar to those which form the pericardial septum in the sinus (Fig. 8, *r*).

The posterior portion of the median nerve remains undivided and terminates in the ganglion of the proventriculus (page 57). This ganglion not only supplies the proventriculus and chyle stomach, but gives off several ganglionated nerves on each side to the salivary glands (page 61).

Further details of structure and the manner in which the ganglion cells are related to the parts they supply will be given in the histological section of this work.

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## APPENDIX TO CHAPTER IV.

### METHODS OF STUDY.

THE great improvements of modern histological research are the perfect fixing of the tissues, the use of a nuclear in the

place of a diffuse stain, dehydration with alcohol and mounting of soft tissues in Canada balsam in the place of fluids, glycerine, and glycerine jelly, which all have a most destructive action so far as the finer details of structure are concerned. The use of serial sections stained after they are cut has almost superseded the old methods of dissociation with needles, although this method is not without advantages, when the tissues are properly fixed. I believe I have tried all the principal methods recommended at various times, but have finally adopted the following almost exclusively.

1. **Fixing.**—The 'fixing' of the tissue elements is of primary importance, and the majority of the preparations I have seen of parts of insects are rendered worthless by defective methods. All the ordinary fixing fluids fail in the Blow-fly larva, owing to the great impermeability of the integument. I have found the following methods good :

1. The integument may be slit up longitudinally under Flemming's solution,\* and the parts removed with fine-pointed glass rods. Preparations of the several tissues should be examined within half an hour or less of their immersion.

2. The living larva may be injected by means of a hypodermic syringe, with a mixture of peroxide of osmium, 1 % solution, and absolute alcohol, 1 part to 20. This is the best preparation for the demonstration of Newport's segment and the stomal discs. Larvæ so prepared may be dissected under water or Flemming's chromo-acetic solution;† or the parts removed may be placed in absolute alcohol, and afterwards mounted.

3. The larvæ may be fixed by heat : a few should be placed in a test-tube with water, heated to the boiling point, and allowed to cool. The opacity of the larva indicates the coagulation of its blood. Larvæ heated in absolute alcohol, Mayer's method,‡ almost always burst. Heating in water is the best method of preparing larvæ for cutting sections, as all the

\* Chromo-aceto-osmic mixture ; an aqueous solution of chromic acid 0.25, osmium peroxide 0.1, and glacial acetic acid 0.1 %.

† The above without the osmium peroxide.

‡ Mitth. Zool. Stat., Neapel, ii., p. 7, 1881.

tissues are perfectly imbedded in the coagulated blood. Sections cut by a mechanical microtome, from heat-coagulated larvæ imbedded in paraffin, were prepared in the following manner.

**2. Imbedding.**—Heat-coagulated larvæ are cut longitudinally or transversely and placed in absolute alcohol for two or three days, transferred to chloroform, and left until they sink. I adopt the following modification of Giesbrecht's method:\*

The chloroform is gradually saturated with fragments of hard paraffin. When it will dissolve no more it is placed in an oven and gradually heated, adding paraffin a small piece at a time, until the temperature of 130° Fahr. is reached; the chloroform evaporates slowly, and sufficient paraffin must have been added in the process to prevent rapid evaporation. The concluding stages are performed in an open vessel. In twenty-four hours or longer the last traces of chloroform have been removed. The imbedding mass is allowed to cool, and the specimen is cut out and prepared for the microtome.

The specimen must be placed in position before the paraffin is allowed to cool.

It is important to perform the whole operation at as low a temperature as will melt the paraffin. Any undue rise of temperature will render the integument horny and destroy the specimen.

All my serial sections were made with the Cambridge rocking microtome.

**3. Staining and Mounting.**—Staining is most satisfactorily effected after cutting the sections. I adopt the following process, which leaves nothing to be desired:

1. The section ribbon should be attached to the glass slip with equal parts of white of egg and glycerine, Mayer's formula.† I effect this as follows:

I spread a thin film of glycerine albumen on the slip by a camel's hair pencil, which has been previously wetted with distilled water. If not wetted the glycerine albumen becomes

\* Zool. Anzeig., p. 483, vol. iv., 1881.

† Journ. of Roy. Mic. Soc., new series, iv., p. 317, 1884.

frothy and the air bubbles remain. Adjust the paraffin ribbon on the slip and bring it everywhere into contact by means of a clean wet camel's hair pencil. Place the slips in an oven at 100° Fahr., and heat to the melting point of the paraffin. Allow the slips to remain at this temperature at least two hours.

Prepare the following baths :

1. Spirit of turpentine.
2. Methyated spirit.
3. Equal parts of methyated spirit and distilled water.
4. Distilled water, 100 c.c., 10 % sol. hydrochloric acid,  
1 c.c.
5. Ehrlich's logwood.\*

1. The slips with the specimens attached are taken from the oven and immersed in bath 1 whilst still hot. They should remain from one to twenty-four hours. Prolonged immersion does no harm, but a trace of paraffin remaining prevents staining. If the bath is not fresh it is as well to place them for a few minutes in a second turpentine bath.

2. The slips are removed from the turpentine and placed face downwards in 2. The turpentine sinks to the bottom of the spirit; a second bath of spirit may be used with advantage. They should remain at least ten minutes. Transfer to bath 3 for a few minutes, and to bath 4 for from five minutes to a quarter of an hour. They should be moved about in bath 4 until the acidulated water lies smoothly on the slip. Pour a

\* I prepare Ehrlich's Logwood (Hæmatoxylin) stain as follows :

Hæmatoxylin Crystals (the best), 2 grms.

Absolute Alcohol, 100 c.c.

Dissolve and add—

Distilled Water and Glycerine, 100 c.c. of each.

Alum, as much as the mixture will dissolve.

Finally add 5 c.c. of glacial acetic acid.

This stain should be kept at least a year in a corked bottle. If kept in a stoppered bottle, the vessel should hold at least 600 c.c., and the stopper should be removed occasionally to change the air. I believe the time necessary to render the stain as good as possible may be much abbreviated by shaking the vessel frequently, and I know its improvement is due to the oxidation of the alcohol. When recently prepared it is useless. For the original formula see *Zeitsch. f. wissensch. Mikr.*, iii., p. 150, 1886, and *Journ. R. Micros. Soc. Lond.*, 2nd ser., vi., p. 1090, 1886.

few drops of 5 over the slide, and cover with a bell glass for an hour or two.

3. Wash well in bath 4, and judge by the colour of the specimens, which should be orange-yellow, not brown, or they are stained too deeply. If too deeply stained leave them in the acid bath until they assume the desired tint. Practice is needed in judging of this.

4. Place the slides face upward in a large vessel, holding half a gallon, of any hard water. The colour of the preparations will gradually change to a brilliant blue—this may require an hour or more—I use ordinary London water.

It is advantageous to place the specimens in a shallow dish, through which a gentle stream of water is flowing for half an hour, as a trace of acid in the albumen film causes the colour to fade. I use a porcelain photographer's bath, and allow the water from the tap to flow in a thin stream into one corner and out of another. Specimens so prepared exhibit perfectly definite nuclear staining.

If thought desirable, a second diffuse stain as neutral carmine may now be poured over the slide and washed off when the preparation is sufficiently stained. I do not think, however, that such double staining serves any useful purpose, as the logwood usually gives sufficient colour to differentiate all the tissues—whilst the double stain often obscures details. The lime salts in the water used is a powerful mordant of Hæmatoxylin. I formerly rendered the water bath feebly alkaline, a glass rod dipped in liq. ammoniæ used to stir the bath is sufficient. Neither soda nor potash should be used, and the advantage of using ammonia is doubtful.

5. Transfer to a bath of 50 % alcohol, and then to a bath of methylated spirit. Wash the slide with a little absolute alcohol—1 c.c. is sufficient—allow it to drain for a moment, and drop clove oil over it with a pipette, moving it as a photographer does a plate he is coating with a film or with varnish.

Drain by setting the slides on end, under a glass shade, on a sheet of filter-paper. If there is any cloud it may be removed

by placing the slides for a few moments in an oven at 100° Fahr.

Clouds are produced by water or alcohol. A water cloud cannot be removed, and depends on the presence of water in the methylated spirit. Alcohol clouds arise from the use of too much clove oil. Clove oil will not dissolve alcohol, but displaces it. Setting the slide on end usually dissipates any alcohol cloud.

The specimens must on no account be allowed to dry at any stage of the process; if they do they are ruined. The greatest danger is after the washing with absolute alcohol. The methylated spirit used must be the best, and entirely free from gum. After draining off the clove oil I mount in Canada balsam dissolved in xylol.

Staining in bulk before cutting may be effected with borax carmine, but is often unsatisfactory. Picro-carmine may also be used. I find that immersion of the part of the larva to be stained in solution 4 for some hours facilitates the penetration of the stain. In no case can an entire larva be satisfactorily stained, as the integument is practically impervious.

Whatever process is adopted, no good can result from improperly-fixed tissues.

## CHAPTER V.

### THE INTEGUMENTAL SKELETON OF THE IMAGO.

#### 1. GENERAL CHARACTERS OF THE EXO-SKELETON IN INSECTS.

WILLIS, as long ago as 1692, recognised certain analogies between the cuticular skeleton of an insect and the osseous skeleton of a vertebrate. Geoffroy St. Hilaire was the chief exponent of the ideas which Willis enunciated, whilst Audouin and his followers, amongst whom the great majority of the present school must be included, persistently regard all such views as misleading. No doubt, as far as details are concerned, the followers of Audouin are right; nevertheless, it must be admitted that analogies exist, in the modern sense of the word, whilst the most recent literature on the subject, the writings of Patten and Gaskell, show that even in the wider sense in which the word analogy was used by St. Hilaire, there is more truth in his theory than has been admitted by the disciples of Audouin.

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**Bibliography.**—The following works, with those quoted on page 7, deal more especially with the external skeleton.

36. SAVIGNY, J. C., 'Mémoires sur les Animaux sans Vertébrés,' premier part, 8vo, Paris, 1816.

This work is the foundation of the present nomenclature applied to the parts of the mouth in insects and arthropods generally.

37. LATREILLE, P. A., 'Observations Nouvelles sur l'Organisation extérieure et générale des Animaux Articulés, et à Pieds Articulés, et application de ces connoissances à la nomenclature des principales parties des mêmes Animaux.' *Mém. du Museum d'Hist. Nat.*, tom. viii., p. 169, 4to, Paris, 1822.

38. AUDOUIN, V., 'Recherches Anatomiques sur le thorax des Animaux

The skeletal structures of insects, both internal and external, undoubtedly consist of indurated cuticle, both the epiostracum and endostracum taking part in their formation. These hardened or chitinized cuticular structures form plates, rings, or complex solid or hollow parts, resembling small ossicles, and are denominated sclerites.

The internal sclerites which form an endo-skeleton are either indurated inflexions of the epidermis, or indurations of the cuticular layer of the alimentary canal, or of the tracheal vessels, yet the former are apparently replaced in some arthropods, by a tissue closely resembling cartilage, as, for example, the ento-thorax in the scorpions; and this tissue is regarded by Lankester\* as of mesoblastic origin—a fact which, taken with many others, indicates a similarity which is not by any means a mere superficial resemblance between the cartilaginous skeleton of a vertebrate and the indurated epidermal skeleton of an insect.

Further, in both sub-kingdoms it is indubitable that the skeletal structures afford the most important morphological characters, and preserve, more or less perfectly, the original segmental character of the embryo in the adult organism. In both sub-kingdoms the skeleton is modified in accordance with

\* 'On the skeleto-trophic tissues and coxal glands of *Limulus*, *Scorpio* and *Mygale*.' *Quart. Journ. Micros. Sc.*, vol. xxiv., new series, 1884.

Articulés et celui des Insectes Hexapodes en particulière.' *Ann. Sc. Nat. Zool.*, tom. i., 1824.

39. AUDOUIN, V., art. 'Insectes,' *Dictionnaire Classique d'Histoire Naturelle*, tom. viii., 8vo, Paris, 1825.

This article gives a very complete résumé of the views of Audouin, which are the basis of the modern nomenclature of the thorax.

40. STRAUS DURCKHEIM, 'L'Anatomie Comparée des Animaux Articulés. A laquelle on a joint l'Anatomie descriptive du Hanneton,' 4to, Paris, 1828.

One of the most masterly memoirs ever published. The nomenclature of the parts is, however, entirely empirical, and founded on supposed analogies with the parts of vertebrates.

41. MIALl AND DENNY, 'The Structure and Life-History of the Cockroach,' 8vo, London, 1886.

This little work is an excellent introduction to the more extended study of the Insecta, and should be read by every student.

the needs of locomotion. Such considerations led Geoffroy St. Hilaire and his followers to apply the names of various parts of the vertebrate skeleton to those of the insect skeleton which, as they conceived, serve similar functions. Although, perhaps, without exception, such terms are not justified, and in a strictly morphological nomenclature must be rejected, their rejection would be exceedingly inconvenient, and would lead to the adoption of many new and unfamiliar terms.

**Definitions.**—In all insects the sclerites of the head, thorax and abdomen, except those of the pre-oral region, form a series of annuli or rings, and correspond more or less closely with the surface of the primitive somites of the embryo; hence their morphological import. As this portion of the skeleton cannot be properly called axial, I shall term it somatic, to distinguish it from the skeleton of the appendages of the metameres, which may be properly termed appendicular. The sclerites of the somatic skeleton are chiefly plates, and the limits of these are marked by seams or sutures.

The appendages of an insect are also segmented, hence the term *Arthropoda*, and the several segments of an appendage are termed joints; this term is therefore used in two distinct senses: it may either mean a segment of an appendage, or the articulation between two sclerites. Ambiguity does not necessarily arise from this usage, although it would be better to adopt a more consistent nomenclature. The segments of an appendage are so generally called joints in works on entomology, that it is difficult to avoid this usage. I shall therefore always speak of the union of two or more sclerites as an articulation, except when the word joint is qualified, as in the expressions ball-and-socket, or hinge-joint, when it may be used without ambiguity in its more usual sense. The different forms of articulation may be classed under two groups, *Sutures* and *Arthroses*.

*Sutures* are seams between the sclerites, and are chiefly seen in the somatic skeleton. *Arthroses* are movable articulations, such as occur in the appendicular parts of the skeleton. A suture may be either a symphysis or a syndesmosis.

**Symphysis** (Fig. 20, 1) signifies the union of two sclerites by an inflected chitinous ridge between them.

**Syndesmosis** (Fig. 20, 2) is the union of two sclerites by a soft, flexible portion of the cuticle. Syndesmoses are frequently imbricate; that is, one sclerite overlaps the other, protecting the soft integument between them from injury.

**Arthrosis.**—An arthrosis is a kind of locked syndesmosis: two joints of an appendage are united by syndesmosis, but processes on the exterior of one fit into hollows on the exterior of the other. These may form a hinge, or peg joint, or, in some

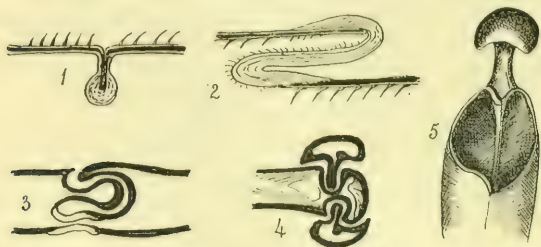


FIG. 20.—The principal forms of Articulation (Diagrammatic): 1, symphysis; 2, syndesmosis; 3, ball-and-socket-joint, from a section of the tarsus of the fly; 4, ginglymus or hinge-joint; 5, coxa, with a hemispherical articular surface, showing its relation to the line of attachment of the syndesmotomic membrane.

cases, a ball-and-socket (Fig. 20, 3, 5). A hinge joint, ginglymus (Fig. 20, 4), admits of flexion and extension in one plane only; a peg joint, of rotation only; and a ball-and-socket, amphiarthrosis, admits of more or less free movement in any direction. There are other forms of articulation, but these do not need special terms for their description; they are generally a modification of one or other of the above.

**Sutures** may be arranged in three classes, in accordance with their morphological value; median, primary, and secondary sutures.

**Median Sutures** are either dorsal or ventral, and are indicative of the bilateral symmetry of the developmental process. They represent the furrow between the two halves of the primitive

band of the embryo in the ventral region and the raphé in the dorsal region, formed by the union of the two lateral halves of the somatopleure on the dorsal surface of the yolk.

**Primary Sutures** are the remains of the inflections of the epiblast between the primary somites of the embryo.

**Secondary Sutures** are either symphyses or syndesmoses, separating the sclerites of a metamere.

**Morphological Considerations.**—The median dorsal sutures are the first to disappear in the more highly-modified types. In the higher forms of the Insecta the median sutures are rarely present, but their position is indicated by complex inflections of the integument in the ventral region. Such are the entothoracic and endocranial processes which support the ganglia of the ventral chain. The consolidation of the somites, which is characteristic of the most highly-modified types, leads to the obliteration, or partial obliteration, of the primary sutures, whilst the secondary sutures become larger and more numerous, and frequently form important syndesmoses. These are especially concerned in the mechanism of flight and the respiratory movements of the thorax. Secondary sutures also often form strongly-marked internal ridges and processes, which afford attachment to muscles and add greatly to the solidity of the external skeleton; thus the secondary sutures appear to take the place of the primary sutures, with advanced complexity. The more highly-developed a part, the more numerous and important are its secondary sutures, and the greater the tendency to the consolidation of several somites, with the consequent obliteration of the primary sutures between them. These laws are exemplified in the structure of the head and thorax, and the confusion which exists in the nomenclature of the sclerites of the cephalic and thoracic skeleton depends mainly on the fact that they have hitherto remained unrecognised.

Although the secondary sutures are very similar in corresponding somites of widely-divergent types of insect, their disposition and number have possibly only an indirect morphological significance, and result from similar adaptive

modifications. In the simpler or more generalised forms each somite is protected by a simple annular sclerite, or by a dorsal and a ventral semi-annulus. The consolidation of the cuticular layers in the higher types commences in the inflected ridges corresponding with the primary and secondary sutures, or in relation with the insertion of the more powerful muscles; hence numerous secondary sclerites occur. These are frequently distinct in the adult nymph or young imago, but are often concealed in the adult imago by large deposits of chitin between them and the hypodermis.

A very important fact, to which I would draw attention, is the close resemblance which exists between an external skeleton developed directly from the epiblast of the embryo and an external skeleton formed entirely from the epiblast of imaginal discs; the secondary sutures in both are as closely related as the primary ones. Whether they first appear in the embryo or in the nymph, they represent the same functional adaptation of the skeleton to the needs of the organism. The same ridges and syndesmoses appear on the wing-bearing segments, whilst no traces of them appear on the wingless prothorax or abdominal somites.

If, as I have already stated,\* it is probable that the larva and nymph states in the Metabola are interpolated stages of development, we might expect to find a greater divergence of structure from that of the primitive type in the nymph and young imago, with a tendency to a return towards the primitive type in the more mature insect; and we actually see a more complex condition of the skeleton in the young imago than in the adult insect. In the vertebrate skeleton each bone, as a rule, is formed from several ossific centres, which subsequently unite with each other. In the young insects there are often several sclerites, which are afterwards united to form a single plate, but the process of union is different: the component sclerites are not usually fused by the gradual growth of each and their subsequent union, but by a continuous deposit of chitinous laminæ on the internal surface of the whole, so that

with advancing maturity there is a tendency to return to a simpler form of skeleton.

A classification of the various sclerites indicative of their morphological significance is not possible with our present knowledge. It is not probable, for example, that any one of the smaller plates which occur in the prosternal region of a young imago in the Diptera represents the sternal plate of a more simple somite, or the prosternum of an archaic insect, nor is there any reason to regard the consolidated prosternum of the adult imago, formed by the union of these several sclerites, as homologous with the more simple prosternum of a more generalised type.

Generally, the sclerites which appear at the earliest period of development are either superficial plates, which are subsequently united by a continuous deposit of chitin on their internal surface, or chitinized portions of inflected folds of integument. In the former case, I shall term them *exo-sclerites*, and in the latter *endo-sclerites*. The continuous deposit of chitin by which these are united with each other I shall term the *scleral matrix*; and the sclerites formed of two or all these elements *compound sclerites*; those which consist of only one element *simple*; and sclerites which are formed entirely from the scleral matrix I shall term *matrix sclerites*. Lastly, certain sclerites occur only in the more generalised forms of insects, such, for example, are the bows of chitin which partially surround the limbs of the Cockroach (*Periplaneta*); these are formed in folds of the syndesmotomic integument between the dorsal plate and the limb. I think it probable that these belong to the limb rather than to the thorax, and that they represent two limb joints between the coxa and the trunk, corresponding to the two basal joints of the limb in some Crustacea. If this be so, they are clearly indicative of an underlying archaic type. They are not present in the more highly modified types of insect, and such sclerites may be termed *evanescent*, as they tend to vanish in the higher forms.

**Apodemes.**—This term was applied by Audouin to endo-sclerites which form lever-like rods on which the muscles act.

Sometimes there is a distinct movable articulation between the apodeme and the plate on which it acts. Such apodemes were distinguished by Audouin as *epidemes*; both terms are useful.

**Endopophyses**, **Entosterna**, and **Diaphragmata** are terms applied to the internal inflections of the skeleton. They are plates of chitin, which form partial septa dividing the body cavity, either giving attachment to the muscles, strength to the skeleton, or support to some of the internal organs. The *diaphragmata* are transverse septa; the *entosterna* are consolidated median sutures in the ventral region. *Endopophysis* is a general term for any internal inflection which has not received a distinctive appellation.

## 2. THE HEAD CAPSULE.

### (a) General Morphology.

The head capsule of an insect may be said to be a subovoid capsule with an anterior opening, the mouth; and a posterior opening, the occipital foramen, with the edges of which the skin of the neck is continuous. It is usually described as consisting of an *epicranium*, which forms the convex upper surface and sides of the head capsule, of a plate on its under surface,

### Bibliography:—

42. LEYDIG, F., 'Vom Bau des thierischen Körpers,' Tübingen, 8vo, heft i., 1864.

43. BALFOUR, 'Comparative Embryology,' Lond., 1881.

44. ROLLESTON'S 'Forms of Animal Life,' 2nd edit. Revised and enlarged by W. Hatchett Jackson. 8vo, Oxford, 1888.

Beside the works on insect Anatomy and Development already quoted, the reader who desires to attain further information on the most recent morphological speculations should consult:

45. GASKELL, W. H., 'On the Origin of the Central Nervous System of Vertebrates,' 'Brain,' vol. xii., pt. 1, 1879.

46. BELLONCI, 'Sur la Structure et les Supports des Lobes Olfactifs dans les Arthropods Supérieurs et les Vertébrés.' *Archiv. Ital. de Biologie*, tom. iii., p. 191.

47. GASKELL, W. H., 'On the Origin of Vertebrates from a Crustacean-like Ancestor.' *Quart. Jour. Mic. Sc.*, vol. xxxi., pt. 3, 1890.

48. PATTEN, W., 'On the Origin of Vertebrates from Arachnids.' *Quart. Journ. Mic. Sc.*, vol. xxxi., pt. 3, 1890.

called the gula, and of a rim surrounding the dorsal and lateral parts of the mouth, termed the epistome.

The upper lip or labrum is attached to the anterior edge of the epistome, and the lower lip or labium is articulated with the anterior edge of the gula.

The great compound eyes occupy a larger or smaller area on each side of the epicranium. Three simple eyes are situated near the median line on its dorsal aspect, and a pair of antennæ are articulated with it in front of, or above the great eyes. Sometimes the antennæ are separated from the epistome by a considerable space, which is properly termed the face.

**Historical Résumé.**—Hitherto the head capsules of different orders have not been compared with sufficient care to establish a uniform and satisfactory nomenclature, and entomologists have contented themselves with regional terms, such as cheeks (*genæ*), forehead (*frons*), and vertex, or have borrowed morphological terms, such as clypeus, rostrum, epistome, labrum, and labium, and applied them without due regard to the homologies of the parts designated. For example, the term clypeus, originally applied by Fabricius to the part now called the labrum, has been used indiscriminately for every part of the dorsal or anterior surface of the head by different writers.

Although numerous attempts have been made to establish a uniform morphological nomenclature, so far as I can judge, the only serious one ever made to differentiate and name the sclerites of the head-capsule is the work of Robineau-Desvoidy [49], and his observations were confined to the head capsule of the 'Myodaires' (*Muscidæ*).

The work of comparative morphologists has been, hitherto, entirely founded on the hypothesis that the dorsal surface of the head consists of the sternal region of several pre-oral somites, and that the antennæ, great eyes, ocelli, and even the labrum, like the mandibles, maxillæ and labium, are modified ventral appendages homologous with the thoracic limbs. Such views rest upon no secure foundation, and have done much to retard the advance of knowledge; they originated from the statements of Savigny, and it is only recently that any

departure from his assumptions has found a place in recognised text-books on morphology.

Balfour [43, vol. i., p. 408], however, says 'the antennæ can hardly be considered to have the same morphological value as the succeeding appendages; they are, rather, equivalent to the paired processes of the pre-oral lobes of the Chætopoda.' And Hatchett Jackson [44, p. 497] states that the head in insects exhibits no trace of segmentation, except the appendages of the three first post-oral metameres.

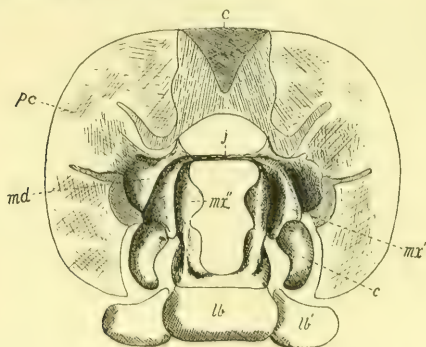


FIG. 21.—The Posterior surface of the Head Capsule of an immature Dragon-fly (*Libellula depressa*): *c*, epicranium; *pc*, paracephalon; *j*, jugum; *md*, *mx'*, and *mx''*, the lateral piers of the mandibular and two maxillary segments; *c*, galea of maxilla; *lb*, labium; *lb'* lateral lobe of labium (galea). The mandibles and lacinæ of the maxilla are not represented.

So far as I know, no one has as yet attempted to show the limits of the somites which bear the mandibles and maxillæ; even those who apparently recognise the non-segmental character of the anterior part of the head capsule are silent on the position and relations of the three post-oral cephalic somites; yet these segments are sufficiently distinct to be easily recognised in the head capsule of immature specimens of *Libellula depressa* and many other insects (Fig. 21).

In order to attain a true conception of the nature of the

head capsule, our investigation must not be limited to a mere inspection of the sclerites of which it is composed, or to a study of the appendages which arise from it. Just as the parts of the skull of a vertebrate have a definite relation to the enclosed nerve centres, so the parts of the head capsule have similar relations to the nerve centres of the insect.

It was formerly supposed, and the idea originated in the mind of Dohrn,\* that the neural surface of a vertebrate and an insect correspond; in other words, that the ventral surface of an insect represents the dorsal surface of a vertebrate. Such an hypothesis is, however, clearly untenable in the light of modern discoveries, and may be said to be practically defunct.

With regard to the nature of the pre-oral nerve centres, they were, and still are, regarded by many, as similar to the post-oral neuromeres, or paired ventral ganglia—a view which I regard as equally untenable, and reject with Dohrn's hypothesis and the theory that the head capsule consists of several pre-oral metameres.

The older writers on insect anatomy recognised strong relationships between the arthropod and the vertebrate brain. Even as lately as 1864, Leydig [42, p. 185] pointed out that in both classes of animals the brain consists of special paired ganglia, arranged in three groups—the fore-brain, the mid-brain, and the hind-brain. To the fore-brain he attributed the function of volition, to the mid-brain visual, and to the hind-brain co-ordinating functions. Faivre stated that in *Dytiscus* these co-ordinating functions are located in the infra-œsophageal ganglia. Leydig included the infra-œsophageal ganglia, and regarded them as the representatives of the hind-brain.

In my Presidential address, delivered at the Annual General Meeting of the Quekett Microscopical Club, February 22, 1889, I made the following statements:

‘The theory of segmentation was formerly applied to the vertebrate skull, and originated in the brains of Oken and Goethe. Professor Huxley, in his lectures on the vertebrate skull, published in London in 1864, disposed for ever, I believe,

\* ‘Ursprung der Wirbelthiere,’ Leipzig, 1875.

of these views, and showed clearly that the skull is developed from parts which do not undergo segmentation. My own researches in the embryology of insects have sufficiently shown me that the brain and head capsule of insects are also developed from structures — the procephalic lobes of Huxley — which undergo no segmentation. I am, indeed, convinced that there are no prestomal segments in insects.

‘Viewed in relation to development, the brain in insects consists of a central ventricle and two hemispheres, which are themselves hollow. The central ventricle contains a transverse and longitudinal commissure, the corpus centrale, and is connected by its posterior wall with the median eyes or ocelli. There is thus a close correspondence between the brains of vertebrates and those of insects. The so-called antennal lobes correspond to the olfactory bulbs, the central ventricle to the third ventricle, and the ocelli to the pineal gland, or pineal eye, where the latter is developed. The hemispheres are cerebral lobes, and the pedunculated bodies are merely isolated convolutions of the surface.’

At that time I thought that such views would be regarded as a return to ideas long laid aside, and I confess I was unable to explain the position of the alimentary canal, which led me to suspect that, however striking the analogy between the two, it must be analogy only.

**Gaskell's Views.**—It was not until I had read Dr. Gaskell's paper on the origin of the central nervous system in vertebrates [45] that a more complete light was thrown upon the whole subject. Still further confirmation is afforded by the papers on the origin of vertebrates from a Limuloid ancestor by Gaskell and Patten [47 and 48] quoted at the commencement of this section.

Both these authors bring a large amount of evidence to show that the brain in the lowest forms of vertebrates corresponds very closely with the cephalic nerve centres of the arthropods.

The most startling consequence of these views is Gaskell's theory that the alimentary canal of the vertebrate is a new

structure, formed on the ventral surface of the embryo, and that the original track of the alimentary canal is represented by the ventricles of the brain and the central canal of the spinal cord, which are the persistent remains of a structure corresponding with the alimentary canal in the Arthropoda.

Although I feel that very great difficulties stand in the way of the complete acceptance of this theory, numerous facts tend strongly towards its verification; and my own observations certainly accord very well with those of the two authors named. These facts were observed by me long before I heard of the views of Patten and Gaskell, and only needed a theory, such as they have put forth, to bring them into accord, and to show that there is a far closer relation between the vertebrate and arthropod types than has been suspected—at least, of late. I therefore avail myself of their views as a working hypothesis.

**Nerve Centres.**—The unexpected discovery of the formation of the primitive archenteron, as a dorsal invagination in the embryo of the larva of the fly (p. 16), is in some sense a confirmation of the theory that the central canal of the primitive nervous system of vertebrates is the morphological representative of the alimentary tract; it has, however, yet to be shown that the primitive neuromeres or ganglionic centres are related to this invagination in insects. Hitherto I have not been able to trace any such relationship, but I regard it as far from unlikely that the cells from which the nerve centres arise are primarily derived from the outer surface of the archenteron. In embryos not more advanced than those represented in the figure, I have been unable to detect any trace of nerve centres, but it is possible that they are derived from the invaginated part of the blastoderm, although they first appear on the inner surface of the ventral epiblast, at a later stage. The dark cellular mass which surrounds the archenteron, and extends into the head, is certainly suggestive of some such relationship.

Leydig held that the infra-œsophageal ganglia are the representatives of the cerebellum and medulla, and it is rather remarkable that Gaskell has not apparently seen that such a

view cannot be maintained if the alimentary tract represents the central canal of the nervous system. The great corpora fungiformia more probably represent the cerebellum. The post-oral metameral ganglia, from which all the true nerves arise, are infra-œsophageal, and probably, with the thoracic ganglia, correspond to the medulla oblongata. The loss of co-ordination due to the destruction of these ganglia is no argument, as it is impossible to destroy them without destroying the peduncles of the supra-œsophageal ganglia.

The manner in which the fibres of each crus diverge and form three bundles has not, so far as I know, been observed by previous writers; these three bundles correspond to the three sections of the brain: the anterior bundle goes to the fore-brain, the middle bundle to the mid-brain, and the great posterior bundle forms the stem of the internal and external calix of the corpus fungiforme.

This divergent arrangement of the nervous cords which form the crura is clearly indicative of an arrangement of the centres in front of the mouth, not in a linear series, but as a divergent series all equally related to the segmental neuromeres.

In the brain of the more generalised Insecta—as, for example, that of the Cockroach (*Periplaneta*)—the trabeculæ (*Balken*) appear to me to represent the thalamencephalon, the cauliculi (*Vorderhorn*) the corona radiata, and the peduncles (*Hinterast*) the superior peduncles of the cerebellum.

The œsophagus lies below the ventricle of the cerebroid

#### DESCRIPTION OF PLATE V.

A series of diagrams illustrating the theoretical structure of the skeleton in insects.

FIG. 1.—Side view.

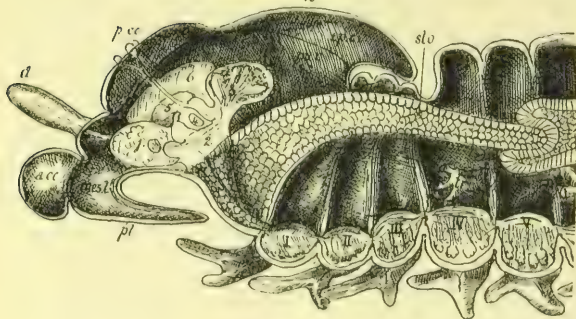
FIG. 2.—Median section.

FIG. 3.—Ventral view, with the integument removed on the right side to show the nerve centres: *a*, antenna; *a cc*, anterior cephaloceles; *e*, compound eye; *epc*, epicephalon; *l*<sup>1</sup>, *l*<sup>2</sup>, *l*<sup>3</sup>, thoracic legs; *md*, mandible; *mx*<sup>1</sup>, maxilla; *mx*<sup>2</sup>, second maxilla; *mes l*, mesolabrum; *pl*, prelabrum; *p cc*, posterior cephaloceles; *pa c*, paracephalon; *s*<sup>4</sup>, *s*<sup>5</sup>, *s*<sup>6</sup>, 4th, 5th, and 6th somites; *st*, stomodæum; I. to VI., neuromeres of the ventral chain; *z*, antennal ganglion; *z*, upper part of the crus of the cerebrum; 3, corpus fungiforme; 4, median commissure surrounded by the central ventricle; 5, cerebroid ganglia; 6, optic ganglia; 7, commissure of the optic ganglia.

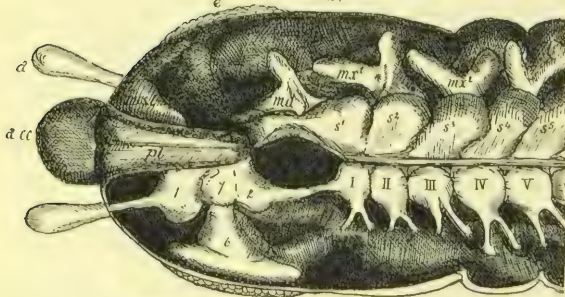
1.



2.



3.





ganglia, and below the median commissure of the optic lobes and corpora fungiformia.

The nerves to the organs of the mouth and face arise from the infra-oesophageal ganglia, whilst those which supply the auditory organ are derived from the sixth or seventh neuromeres, or segmental ganglia, which in the insect are the posterior thoracic ganglia.

**Biramous Appendages.**—If, as Dr. Gaskell suggests, the limbs of the arthropod correspond with the visceral arches of the vertebrate, and the branchial clefts are the spaces between them, we should have seven such clefts between the auditory capsule and the mouth, representing the cephalo-thoracic limbs, corresponding with seven pairs of cephalic metameral nerves as the primitive number in vertebrates. That no vertebrate is known in which these arches exist does not, however, militate against the argument, as the persistence of the cranial nerves renders it certain that a number of somites have disappeared in the process of evolution.

The double character of the embryonic appendages in the Crustacea, and in the maxillæ of insects, as well as in the thoracic limbs of the rudimentary fly nymph, is certainly very suggestive of the double character of the pterygomaxillary arch, or even of the hyomandibular in vertebrates.

It is true Balfour [43, vol. i., p. 542) states that in insects double or biramous appendages never exist; but this statement is certainly erroneous, though, except in the nymph of the Diptera, the thoracic legs have not hitherto been seen in insects in the biramous stage. I cannot doubt that the biramous thoracic feet of the fly nymph, described by Weismann, and seen by myself, are indicative of a primitive biramous condition.

**Development and Morphology.**—The head of an insect consists undoubtedly of a pre-oral and a post-oral portion, and the latter is formed from three segments (Pl. V., Figs. 1, 2, and 3), whilst the former, although divided into three distinct regions, is only segmented in a very different sense; it does not exhibit a series of metameres.

The pre-oral part is either developed from a cap of blastoderm, the head-cap, or from a single pair of imaginal discs, which represent the invaginated head-cap and procephalic lobes. The structure of the head is also the same, whether it is developed from the blastoderm directly, or from the invaginated imaginal discs.

The procephalic lobes (Pl. V., *pa c*) are thickened lateral portions of the head-cap, and are connected with the segmented post-oral primitive band by a pair of crura which surround the stomodæal pit. The procephalic lobes bear the great eyes (*e*) and the antennæ (*a*), which are undoubtedly olfactory organs.

The head capsule will be seen therefore, to consist of a segmented portion behind, which I term the 'metacephalon,' and laterally of two plates in front of the metacephalon, bearing the great eyes and the antennæ; these I term 'paracephala' (Pl. V., *pa c*). The paracephala are united in front, and form the epistomum and the labrum (*pl*). The median region behind the epistomum, or metalabrum which I regard as a preferable term, exhibits three distinct parts; two of these are frequently bladder-like swellings, the anterior and posterior cephalocele (Pl. V., *a cc* and *p cc*). The facial region is developed from the former and the forehead from the latter, the simple eyes are situated in the forehead, or on the posterior cephalocele. Behind the forehead there are two plates, which extend forwards from the metacephalon; these form the epicephalon.

That portion of the procephalic lobe which lies in front of the crus unites with its fellow, and curves downwards and backwards over the mouth, forming the prefacial region (*mes l* and *pl*). So that there is a close resemblance between the crura of the profrontal lobes and the trabeculæ cranii of the vertebrate.

The anterior and posterior cephalocele correspond with the thin portion of the blastoderm which intervenes between the procephalic lobes. The posterior cephalocele is the forehead (*Vorderkopf*) of the German embryologists. In the Dragonflies it persists as a bladder-like swelling, on which the simple

or median eyes—ocelli—are situated. When it is closed by plates of chitin these are usually, a triangular sclerite sometimes obviously divided into three, which bears the ocelli, the 'epifrontal sclerite' (*Mihi*), and two flat plates below or in front of the epifrontal, which I term 'mesofrontals.' The median eyes, or ocelli, correspond very closely with the so-called pineal eyes of the lower vertebrates, and just as the pineal eyes are evanescent, so the median eyes of insects are frequently absent. They are very rarely present in the Coleoptera; but I have one specimen of *Cicindela maritima* with a pair of ocelli, the only specimen I have seen in which they are present.

In the Muscidæ the frontal sac consists of a great part of the posterior cephaloceles withdrawn into the interior of the head, between the meso-frontals and the antennal ridge, a ridge developed by a process from each profrontal lobe between the two cephaloceles.

The anterior cephalocele persists in the Dragon-flies and in the Homopterous Hemiptera as a very large sub-hemispherical protuberance, but it is more generally closed by a pair of plates, which subsequently meet in the middle line, forming the facial plate. In front of the facial plate the profrontal lobes meet in the middle line, and form the base of the upper lip, or labrum; this portion of the profrontal lobes curves back over the mouth. I term the whole of that part of the head which is formed by the union of the profrontal lobes in front of the anterior cephalocele the 'prefacial region.' It is usually distinctly divided into three parts—the meta-, meso-, and prelabrum. The former is termed the epistome; the mesolabrum forms a rostrum in many insects; the prelabrum is commonly known as the labrum.

In the Diptera, at least, the pro-, meso-, and metalabrum are generally each protected by a pair of lateral sclerites, which are at first distinct, but become fused in the mature insect.

It will be seen, therefore, that not only are there three primary divisions of the cephalic nerve centres, excluding the cephalic neuromeres, but three corresponding enlargements of the primitive brain case or head capsule. Plate V. shows the

relations of these parts and of the segmental region of the head.

The figures are diagrammatic, and only intended to give the results of a long series of observations, made partly on embryos and partly on various adult and larval insects. The head capsule is represented in its embryonic condition, and the nerve centres in the form they assume in the adult of the most highly differentiated Insecta.

I regard the anterior cephalocele (*a cc*) as the vesicle of the olfactory lobes (*l*), the posterior cephalocele (*p cc*) as the vesicle of the cerebral hemispheres (*h*) and their median ventricle. The epicephalic region (*ep c*) is probably more complex, and corresponds with the optic commissure, the corpora fungiformia (*f*), and the dorsal arches of the first three ventral neuromeres (I., II., III.), whilst the great optic lobes (*o*) apparently belong to the paracephala (*pa c*). The latter frequently overlap the segmental parts of the head capsule, especially in the Orthoptera, thus bearing some resemblance to the opercula in fishes.

In the Fly-nymph the median parts of the head capsule lie in a deep cleft between the two paracephala, and in close proximity to the ganglia with which they correspond, so that the head appears to be open in the middle line; but sections show that this appearance is due to the deep infolding of the inner edges of the paracephala.

I shall hereafter show that the paired lateral invaginations of the epiblast, from which it is stated the pre-oral centres are developed in some arthropods, are sensory vesicles—a view which is borne out by the development of the compound eyes, thus establishing another relation between the arthropod and the vertebrate.

The nature and relations, as well as the developmental history, of the nerve centres and sense organs will be fully discussed in the sections devoted to the nervous system.

### b. On the Nomenclature of the Sutures and Sclerites of the Head Capsule.

Before attempting a detailed description of the head capsule of the Blow-fly, I shall define the terms which may be very generally applied to the sutures and sclerites which are found in the head capsule of an insect.

In the Earwig, *Forficula* (Fig. 22), or the Cockroach, the median epicranial suture will be readily recognised (Fig. 22, *v x*). Its anterior extremity bifurcates and marks the anterior limit of the paired epicephalic sclerites.

The diverging branches of the epicranial suture I term 'epifrontal sutures' (Fig. 22, *x, y*). On either side of the epicranial suture a faint suture (*u y t*) separates the paracephalon from the median region of the head capsule. The antenna is articulated either directly or through the medium of a small sclerite—the torulus (*t*)—with the anterior border of the paracephalon (*p*).

Immediately above the antenna in *Forficula*, and in many other insects, there is a dark spot; it marks the junction of the internal skeleton of the head with the anterior border of the paracephalon. The occipital foramen is surrounded by a scleritic ring—the metacephalon, which consists of the dorsal and lateral parts of the three first post-oral somites.

The sternal portion of these somites forms the gula, or greater part of the lower surface of the head, in the Coleoptera. In the Earwig and many Orthoptera, however, the gula is apparently internal. Although the axis of the head is more or less vertical, the gula remains nearly horizontal, and is concealed by the mandibles and maxillæ; under these circumstances it is little developed in the middle line, but assumes the form of two lateral bars, which support the mandibles and join the paracephala in front. These lateral bars are, in part at least, developed from the crura of the procephalic lobes (Fig. 22, *z, g*).

The base of the labium, (Fig. 22, *l, mx<sup>2</sup>*) forms with the cardines of the maxillæ (Fig. 22, *l, mx<sup>1</sup>*) the greater part

of the under surface of the head — this I term the ‘pars basilaris.’ The lateral parts of the metacranial annuli some-

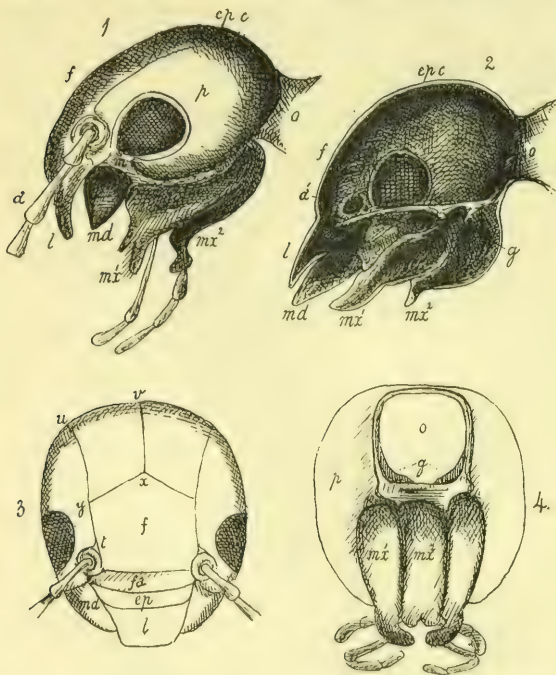


FIG. 22.—The Integumental Skeleton of the Head of an Earwig (*Forficula auricularia*): 1, lateral aspect; 2, interior of one lateral half; 3, anterior, and 4, posterior aspect: a, antenna; cp, epistome; cp c, epiccephalon; f, frons; fa, face; p, paracephalon; g, gula; l, labrum; md, mandible; mx¹, maxilla; mx², labium; o, occipital foramen; t, torulus. Sutures: v x, mesocranial; x y, epifrontal, and u y t, paracranial sutures.

times form piers for the support of the lateral appendages of the mouth. A cotyloid cavity exists on either side of the

occipital foramen, which articulates with one of the thoracic (*cervical*) sclerites. This I term the 'condyle.'

The frontal region (Fig. 22, *f*) extends from the epifrontal sutures to the antennal ridge, which is sometimes produced as a salient rostrum—the antennal rostrum. The face (*fa*) extends from the antennal ridge to the epistome (*ep*).

The frontal and facial regions are often covered by secondary scleritic plates, but are developed respectively from the posterior and anterior cephaloceles. Both regions are represented by hemispherical swellings in the Dragon-flies, and one or other retains this embryonic character in many insects.

**The Internal Skeleton of the Head.**—The gula often supports a saddle-shaped endocranium, on which the infra-œsophageal ganglia lie, corresponding with the furca of the thoracic sterna; it is, however, frequently rudimentary or entirely absent. The remaining endocranial sclerites are the fulcrum and the scleral ring, which will be described hereafter, and the jugum (Figs. 21 *j* and 24 *ju*), a chitinous bar, formed of two lateral halves, springing from the inner edge of the occipital foramen. The jugum assists in supporting the tentorium, on which the supra-œsophageal nerve centres rest.

### c. The Head Capsule of the Blow-fly.

The head capsule of the adult imago (Fig. 23, 1 and 2) of the Blow-fly is comparatively thin—a characteristic shared by the majority of the Diptera. It exhibits a convex anterior and a conically concave posterior surface. The proboscis hangs from its inferior surface, and is capable of being withdrawn into the lower part of the head capsule.

The line of junction between the anterior and posterior surfaces of the head capsule I term the 'crista,' and its central

#### Bibliography :—

49. ROBINEAU-DESVOIDY, J. B., 'Essai sur les Myodaires.' Mém. de l'Institut de France, Sc. Math. et Physiques, tom. ii., 1830.
50. MENZIEB, M. A., 'Ueber das Kopfskelet und die Mundwerkzeuge der Zweiflügler.' Bull. de la Soc. Imp. des Nat. de Moscou, tom. lv, 1880. Abst. in Journ. Roy. M. Soc., ser. ii., vol. i., p. 236.

point the 'vertex.' A vertical line, joining the vertex and the axis of the extended proboscis, may be called the 'major axis' of the head, and the axis of the body prolonged may be termed its 'minor axis.'

The forehead lies between the great eyes. It is broad and

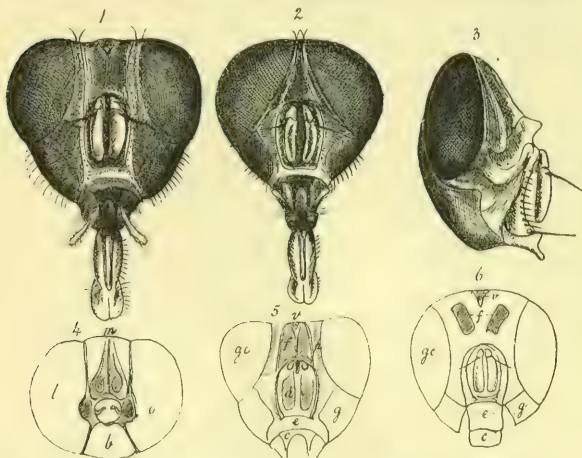


FIG. 23.—1 to 5, The Head of the Mature Imago of the Blow-fly; 6, the Head of *Stomoxus calcitrans*. 1, anterior view of the head of the adult female; 2, anterior view of the head of the adult male; 3, lateral view of the head of a semi-mature male; 4, posterior, and 5, anterior view of the head capsule; 6, anterior surface of the head capsule of *stomoxus*: *b*, pars basilaris; *c*, clypeus; *d*, mesofacial; *e*, epistome; *f*, mesofrontal; *g*, gena; *gc*, compound eye; *l*, lateral plate or posterior part of paracephalon; *m*, mesocranial plates; *p*, parafrontal; *v*, vertex and epifrontal plate.

trapezoidal in the female, and narrow and triangular in the male. In the male the whole head is smaller, and the eyes are more obliquely placed.

Seen from in front, the head capsule of the mature imago exhibits the following parts: the frons, the face, and the epistome in the middle line; with the anterior margins of the paracephala and the great, or compound, eyes on either side.

The **Frons** exhibits three sclerites, a triangular epifrontal, and two subquadrate frontals (Fig. 23, 5, *f*). The three simple or median eyes are situated near the angles of the epifrontal. On either side of the frontal plates there is a narrow sclerite, the parafrontal; it is formed in the anterior edge of the paracephalon.

The **Face** assumes the form of a semi-elliptical shield; it is bounded above by the antennal ridge, and below by the epistome; the large third joints of the antennæ almost conceal it.

Two sclerites are developed in this region—my mesofacials, the foveæ of Desvoidy; these are distinct in the young imago, but become subsequently fused into a single plate (Fig. 24, 1, *mf*).

The **Antennal Ridge** is a distinct sclerite in the young imago, continuous with the facial edge of the paracephalon; it presents a median process, which descends between the antennæ, with a deep emargination, on either side. This ridge corresponds with the toruli and the antennal rostrum; it is distinct in the young imago, but becomes fused with the mesofacials in the adult (Fig. 24, 1, *r*).

The lunula is seen immediately above the antennal ridge.

The anterior edges of the paracephala overlap the face slightly, and form a setigerous chitinated fold on either side of the face; these are the facialia of Desvoidy.

The **Epistome** (Fig. 23, 5, *e*) is but little developed in the Blow-flies; it consists of a narrow, somewhat salient, ridge, joining the facialia below the face. In the Syrphidæ it forms a large beak-like shield, in which several distinct paired sclerites are developed. The epistome in the Cicadæ is very similar to that of the Syrphidæ.

The **Paracephala** exhibit three distinct sclerites in front, the parafrontals, the facialia, and the genæ. The latter appear to be the anterior and lower part of the great lateral plates of the head, extending forward beneath the great eyes. Fig. 23, 3, exhibits a lateral view of the head of an immature imago; the folds of the paracephala, from which the parafrontals, the antennal ridge, the facialia and the epistome are subsequently developed, are very distinctly seen.

The **Antennæ** hang vertically in front of the mesofacial plates; they are usually said to consist of three joints and a bristle. They are really six-jointed, as Desvoidy pointed out, with a greatly enlarged third joint, the three terminal joints being reduced to the form of a three-jointed bristle. The large third joint is cylindroid, and slightly prismatic. It contains a complex sensory organ, which is undoubtedly olfactory (see 'Sensory Organs').

The **Posterior Surface** of the head capsule consists of the

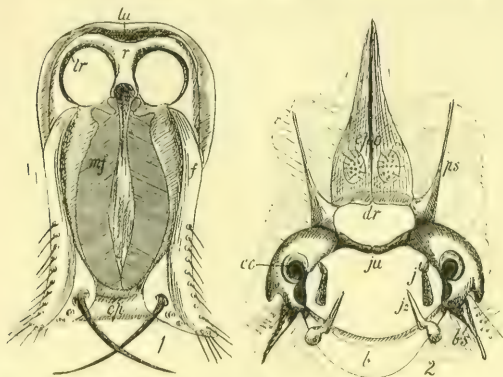


FIG. 24.—1, The Face of the Blow-fly: *ep*, epistome; *f*, facial edge of paracephalon; *lu*, lunula; *mf*, mesofacial plate; *r*, rostrum; *tr*, torulus. 2, the Metacephalon of the same: *b*, basal sclerite or gula; *bs*, basal suture; *cc*, cotyloid cavity; *dr*, dorsal ring; *ep o*, epioccipital sclerites; *j*<sup>1</sup> and *j*<sup>2</sup>, first and second jugulares; *ju*, jugum; *ps*, paracephalic suture.

posterior part of the paracephala (Figs. 23, 4, 1, and 24), the occipitals of Menzbier, the epicephalon (*m*), the pars basilaris (*b*), and the metacephalic ring surrounding the occipital foramen.

The occipital, or metacephalic, ring (Fig. 24) consists of two lateral parts, and of a dorsal and a ventral arch.

The lateral parts are concave externally and convex internally; they each give off a process to form the jugum, and are

continuous with the sclerosed ridges between the paracephala and the median region of the head capsule. The ventral arch is a narrow plate, which probably represents the gula. The dorsal arch forms the basal edge of the two epi-occipital plates.

The epi-occipital plates are triangular; they are united in the median line by a strong ridge-like suture. Each exhibits a slight hollow near its base, covered by fine setæ.

I have been unable to determine whether these plates are part of the metacephalic ring, or whether they belong to the non-segmental region of the head capsule.

A fossa, the cotyloid cavity, in the external surface of the lateral part of the metacephalic ring, articulates with the condyles.

The ventral arch is at first distinct, but is subsequently fused with the pars basilaris. The structure of the metacephalic ring has a striking analogy with that of the occipital bone in vertebrates, as the ventral arch is obviously comparable with the basi-occipital, the lateral parts articulating with the neck, with the ex-occipitals, and the epi-occipital plates with the epi-occipital.

**The Internal Skeleton of the Head** is exceedingly rudimentary, if the scleral ring, to be described with the compound eye and the cephalo-pharynx which belongs properly to the proboscis, be excepted. It consists of a jugum and of a pair of slender rod-like sclerites, entocephala, which I think probably represent the lateral bars already described in the head capsule of the Earwig (page 117).

**The Jugum** is formed by the union of two stout curved processes, one arising from the upper and inner angle of each lateral part of the occipital ring. When seen from behind, the jugum apparently divides the occipital foramen into an upper and a lower opening, but it really lies in a plane a little anterior to the foramen. It assists in supporting the tentorial membrane, an incomplete septum formed chiefly by a network of tortuous tracheal vessels, which extends from the jugum to the entocephala and the lower margins of the great eyes.

**The Entocephalon** is a slender rod-like sclerite on each side, which is not easily demonstrated, as it usually falls out when

the heads are being prepared. It commences between the lateral part of the occipital ring and the pars basilaris, and extends forwards in the tentorium towards the upper edge of the epistome. It is more fully developed in the Syrphidæ and in Volucella, in which Künckel d'Herculais figures and describes it [25, Plate XII., Fig. 1, *c*, and p. 88] as arising from the junction of the pars basilaris with the occipital ring and extending forwards to the anterior and lower margin of the compound eye, its upper edge giving off a curved process to the upper margin of the epistome. In the true flies the whole is such a slender rod, and so easily detached from both the occipital ring and the epistome, that I have generally failed to find it, and have never actually traced it to the epistome. It is mentioned by Menzbier [50].

**The Immature Head Capsule.**—The head of the imago, when it first emerges from the pupa case (Fig. 25), has the form of a cone with a convex base; the antennæ are placed on its under surface, and the proboscis, which is not capable of retraction, lies on the breast between the legs, like the rostrum of an hemipterous insect. The vertex is the most anterior part; the major axis of the head is nearly horizontal (Fig. 25, 1 and 2), and makes an acute angle with the minor axis. At first the frontal sac (*fs*), or posterior cephalocele, is capable of enormous extension, so that it frequently appears larger than the rest of the head. The posterior surface of the head capsule is convex instead of concave, and the whole, if we except the greatly distended frontal sac, is much smaller than the head of the adult insect.

The frontal sac is distended by the contraction of the thorax and abdomen, which drives the blood of the insect into it; by this means the operculum of the pupa case is separated, allowing the insect to escape.

During the subsequent evolution of the head the anterior part of the frontal sac is withdrawn into the head capsule, leaving a curved fissure, the lunula, between the antennal rostrum and the forehead. This fissure is permanent, and communicates with the cavity of the withdrawn frontal sac.

The revolution of the major axis takes place as a result of the withdrawal of the frontal sac into the interior, and the flattening of the posterior surface of the head capsule. During these changes the proboscis becomes further developed, and is gradually retracted within the head capsule.

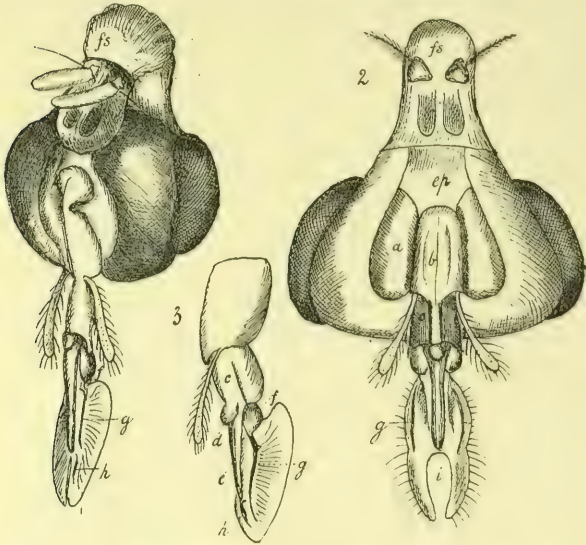


FIG. 25.—The Head and Proboscis of the mature nymph: 1, lateral view; 2, lower surface; 3, lateral view of the proboscis: *fs*, frontal sac; *ep*, epistome; *a*, lateral fold of rostrum; *b*, clypeus; *c*, palpigerous scale; *d*, swelling between meso- and prelabrum; *e*, prelabrum; *f*, discophore; *g*, furca; *h*, discal sclerite; *i*, cleft in the anterior margin of the oral sucker.

It is generally stated that a lunula is characteristic of all the cycloraphic Diptera; in some, however, the frontal sac is not withdrawn into the head, but becomes greatly reduced in size, and remains external, or becomes obliterated by the great development of the frontal sclerites. Künckel d'Herculais

[25] says there is no frontal sac in Volucella or the Syrphidæ; in these insects a slight hemispherical swelling occupies its place, and the lunula, instead of being a fissure, is a mere fold in its lower margin. The head capsule in the flies is very large in comparison to the cephalic nerve centres; the greater part of its cavity is occupied by large air-vessels, the much-folded frontal sac, and the proboscis, when the latter is retracted.

There is, apparently, a close relation between the size of the frontal sac in the mature insect, and the power of retracting the proboscis; those forms in which the proboscis cannot be retracted have apparently no persistent frontal sac. It appears probable that the sac is compressed when the proboscis is retracted, and distended when the proboscis is exerted.

When the imago first escapes from the pupa the only sclerites which are developed are the occipital ring and the sutural ridges connected with it, the epioccipital plate, the frontalia, the antennal ridge, the epifrontals, the mesofacials, and sometimes the mesofrontals, as minute sclerosed points.

The synonymy of the parts of the head capsule is as follows:

**Epicranium**, Straus Durckheim. Upper head (Oberkopf). Burmeister.

**Paracephala**, Mihi. Side of the head, Newport. Lateral plates of the head, Mihi, 1870. Part of the epicranium, Straus Durckheim. They include the occipitals of Menzbier.

**Frons**, Menzbier. Vertex and frontalia of Robineau-Desvd.

**Face**, Clypeus, Burmeister. Antennal fossæ, Robineau-Desvd. Hypostoma, Meigen and Bouché. Clypeus posterior, Newport.

**Epicephalon**, Mihi. Part of epicranium, Straus Durckheim and Menzbier. Cerebrale, Robineau-Desvd.

**Epistomum**, Robineau-Desvd. Clypeus anterior, Newport.

**Metacephalon**, Mihi. Halsband, Menzbier.

**Pars basilaris**, Mihi. Submentum, or gula.

**Gula**, Kirby and Spence.

The terms 'pars basilaris' and 'gula' are usually considered synonymous.

## 3. THE EXO-SKELETON OF THE PROBOSCIS.

## a. General Morphology.

The proboscis of the Blow-fly and the mouth organs of the Diptera were favourite objects of study amongst the first pioneers in microscopical research. Swammerdam, Leeuwen-

**Bibliography :—**

51. ROFFREDI, M., 'Mémoire sur la Trompe du Cousin et sur celle du Taon dans lequel on a donne une description nouvelle de plusieurs de leur parties. Avec des remarques sur leur usage, principalement pour la succion.' Misc. Taurinensia, tom. iv., Turin, 1776-79.
52. ERICHSON, WILHELM FERDINAND, 'Entomographien; Untersuchungen in dem Gebiete der Entomologie.' 1. Ueber Zoologische Charaktere der Insecten, Arachniden und Crustaceen. Berlin, 1840.
53. BRULLÉ, 'Recherches sur les Transformations des Appendices dans les Articulés.' Ann. Sc. Nat., ser. iii., tom. i., Zool., 1844.
54. BLANCHARD, E., 'De la Composition de la Bouche dans les Insectes de l'Ordre des Diptères.' Compt.-Rend., tom. xxxi., pp. 424-27, 1850, Paris.
55. GERSTFELDT, G., 'Ueber die Mundtheile der Saugenden Insecten. 8vo, Dorpat, 1853.
56. HUNT, 'The Proboscis of the Blow-fly.' Quart. Journ. Microsc. Sc., vol. iv., 1856, London.
57. MAYER, 'Ueber ein neu entdecktes Organ bei den Dipteren.' Verhand. Naturh. Versamml. Preuss. Rheinl. und Westfalen Sitzungsberichte, Bd. xvi., p. 106. Bonn, 1859.
58. SUFFOLK, W. T., 'On the Proboscis of the Blow-fly.' Month. Micros. Journ., vol. ix., 1869.
59. LOWNE, B. T., 'On the Proboscis of the Blow-fly.' J. Quekett Micr. Club, vol. i., p. 126, 1868.
60. LOWNE, B. T., 'Further remarks on the Proboscis of the Blow-fly.' J. Quekett Micr. Club, vol. i., p. 190, 1868.
61. ANTHONY, 'The Suctional Organs of the Blow-fly.' Month. Micros. Journ., vol. ix., 1869.
62. LOWNE, B. T., 'The Anatomy and Physiology of the Blow-fly.' 8vo, London, 1870.
63. GRABER, V., 'Ueber den Schlundmechanismus der Arthropoden.' Amtl. Ber. d. 50 Versamml. Naturforsch. und Aerzte, München, 1877.
64. MACLOSKIE, 'The Proboscis of the House-fly.' Amer. Nat., vol. v., pp. 153-161, 1880.

hoeck, Reaumur, and the Abbé Roffredi exercised great patience in the investigation of these organs; but it was only after the genius of Savigny showed the nature of the morphological problems involved, and made the principle clear that the mouth organs of all Arthropods possess a common underlying type, that the Dipterous mouth became a puzzle, affording exceptional scope for speculation to those who regard Morphology as a field for the exercise of their ingenuity.

Savigny, after giving a careful exposition of the structure of the mouth in the Lepidoptera, says, 'I believe I may assert that the mouth of the Diptera is formed of the same parts as that of the Hymenoptera' [36, p. 11], and having described the mouth of the Hymenoptera in general terms, but without detail, he adds, 'The same organs are found separately or united in the mouths of the Diptera. The lower lip exists in nearly all; it forms the proboscis properly so-called. The maxillæ also almost always exist; they are the parts which support the palpi, so that the Diptera have maxillary, but no labial palps. When the maxillæ disappear, as in the true flies, it is because they are united with the lower lip. The mandibles are only present in some genera. They are, for example, very distinct in the Tabanidæ, where they form two very fine

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65. MEINERT, 'Sur la Conformation de la Tête et sur l'Interprétation des Organes buccaux chez les Insectes.' *Entom. Tidskrift*, vol. i., pp. 147, 150, 1880.
  66. MEINERT, 'Sur la Construction des Organes buccaux chez les Diptères.' *Ibid.*, pp. 150-153.
  67. MEINERT, 'Fluernes Munddele (Trophii Dipterorum).' Kjobenhavn, 8vo, 1881, with 6 plates.
  68. DIMMOCK, GEORGE, 'The Anatomy of the Mouth Parts and of the Sucking Apparatus of some Diptera.' Small 8vo, Boston, 1881, with 4 plates.
  69. BECHER, E., 'Zur Kenntniss der Mundtheile der Dipteren.' *Denksch. Wien. Acad., Math. Nat. Kl.*, Bd. xlv., 1882. Gives the literature of the subject very fully.
  70. KRAEPELIN, K., 'Zur Anatomie und Physiologie des Rüssels von Musca.' *Zeitsch. f. w. Zool.*, Bd. 39, 1883.
  71. LOWNE, B. T., 'On the Head of the Blow-fly Larva and its relation to that of the Perfect Insect.' *Journ. Quekett Micr. Club*, ser. ii., vol. iii., p. 120, 1887.

bristles. The hypopharynx\* and the epipharynx are also converted into bristles, and the labrum is a bristle on a larger scale, which covers all the others.'

Savigny produced no evidence in support of these statements, yet they have been almost universally accepted; neither, so far as I know, has anyone adduced any in the seventy years which have elapsed since the publication of his work. Savigny did prove, however, and proved in a very masterly manner, that the paired mouth organs of insects, the mandibles, maxillæ and lower lip, or labium, are homologues of the thoracic legs, and that in the highly modified suctorial mouth of the Lepidoptera there is a great development of the maxillæ, with a corresponding reduction in the magnitude and complexity of the labium and mandibles.

In the Diptera the only reason for regarding the terminal portion of the proboscis as a modified labium or lower lip is its position, and this is no evidence of its nature from a morphological point of view.

The labium of an insect is not merely a lower lip; it is something more. It is a lower lip formed by the union of the second pair of maxillæ.

As we ascend from the less to the more highly modified Arthropoda, there is a tendency to the reduction of the number of post-oral somites developed in the head. Amongst the Crustacea the number of cephalo-thoracic metameres is in excess of that in insects. The three pairs of ventral appendages in Gammarus, which follow the mandibles, will be seen to be all alike, except that the third pair are united to form a lower lip. In the most generalised Insecta the second pair are united, and there is no third pair. In the highly modified Lepidopterous type the second pair of maxillæ are rudimentary, and the first pair form the large suctorial apparatus, whilst the mandibles are rudimentary or absent.

Before I undertook the investigation of the manner in which

\* The statement made by me on page 44, 'The ligula has no relation to the hypopharynx of Savigny,' should have been, *The ligula is not a hypopharynx in the sense intended by Savigny, although he mistook it for one.*

the mouth is developed in the Diptera nothing was known with regard to it. Weismann failed to detect the rudiments of the proboscis in the young nymph, and although Künckel d'Herculais speaks of the appendicular discs of the head, and actually figured them in the resting larva of *Volucella*, he gives but one figure in which I can recognise the position and relations of the maxillary discs [25, Pl. 7, Fig. 1, *ff*], and in the description of the plate he refers to them as the rudiments of the antennæ. He did not, therefore, recognise their real nature.

I have already described the maxillæ of the Blow-fly larva (page 37) and the stomal disc. It is from the hypodermis of the stomal disc that the disc at the extremity of the proboscis originates, and as the second pair of maxillæ are easily seen in the embryo lying between and behind the first pair, on which the rudimentary stomal disc is apparent, it is plain that the terminal portion of the proboscis of the imago is developed from the first, and not from the second pair of maxillæ.

Robineau-Desvoidy is the only author who, so far as I know, arrived at conclusions which my researches enable me to endorse, but, unfortunately, he gives no reasons for his statements, which have received little attention. He says, 'The proboscis of the Diptera, in my opinion, is not formed by the lower lip, as in the Hymenoptera, but by the maxillæ. In the Muscidæ it is usually membranous, sometimes solid and tri-articulate. The more or less solid piece which covers the groove on the dorsal surface of the proboscis is the labrum or upper lip' [49, p. 12]. Desvoidy, however, says in the same paragraph, 'Its base is enveloped by the base of the labium, of

#### DESCRIPTION OF PLATE VI.

One lateral half of the Proboscis of the Blow-fly divided in the middle line and seen from the cut surface: *ps*, the palpiger; *p*, the palpus; *pl*, prelabrum; *l*, ligula; *pa*, paraphysis; *ds*, discal sclerite; *th s*, thyroid sclerite; *ep f*, epifurca; *s s*, sesamoid sclerite; *st*, stomal or hypoglossal sclerite; *s v*, salivary valve; *f*, fulcrum; *tr*<sup>1</sup> to *tr*<sup>4</sup>, tracheæ; *m*<sup>1</sup> to *m*<sup>8</sup>, muscles; *s g*, salivary gland of the oral disc. Part of the rostrum only is represented. *s s* to *ep f* is the haustellum, consisting of the theca, prelabrum and disc.





which the palpi are always developed.' He regards the palpi of the Diptera as labial, and not as maxillary, a conclusion which appears to me to be unwarranted. They are, without the slightest doubt, maxillary palpi.

If the proboscis of the Diptera represents the first, and not the second, pair of maxillæ, the four-jointed sheath of the Hemiptera must unquestionably have the same morphological value.

I have repeatedly examined the mouth organs of the larger Cicadæ, and the conclusion at which I have arrived is, that the sheath exhibits no indications of its morphological identity with either the labium or the maxillæ which would enable one to judge whether it represents the one or the other; but there is no evidence that both pairs of maxillæ are developed, or that either pair of setæ should be identified as representatives of the first pair.

Just as nearly everyone has accepted the statement that the greater part of the proboscis of the Diptera represents the labium, so they have accepted the statement that the sheath of the lancets in the Hemiptera is a modified labium; yet this view which Savigny initiated depends mainly upon the supposed identification of the second pair of setæ with the maxillæ. Against this identification, I would observe, there is no evidence that a seta can be homologous with a maxilla, and the manner in which these setæ are connected with the head shows at once that they are not the maxillæ. Latreille identified them with the terminal lobes of the maxillæ, a much more correct view of their homology.\*

Before entering upon a detailed examination of the proboscis with a view to elucidate its real nature from a morphological point of view, it is essential to acquire a definite idea of the nature and structure of the labium and maxillæ in insects.

**The Labium.**—Erichson [52] discusses the mouth parts of insects; in especial relation to the structure of the labium, or lower lip, he says:

'The third pair of jaws, in the Insecta, form a considerable

\* Cuvier, '*Règne Animal*,' Nouvelle edit., 8vo, Paris, 1829, tom. v., p. 190.

portion of the under-lip, which is composed of these united with the mentum, or chin, and the tongue (*ligula*). The third pair of jaws have the chin behind and below them, and the tongue above and before them (between their terminal lobes on their oral surface) and always united with them through its coalescence with the remarkable labial palpi.'

The nature of this tongue has led to much discussion. Savigny called it the 'hypopharynx,' and erroneously supposed it to be a mere process of the floor of the pharyngeal cavity. It is really always a tongue-like process of the floor of the mouth, which either overhangs or surrounds the extremity of the duct of the great salivary (lingual) glands, and it arises from the base of the labium. It may be fleshy as in the Cockroach, reduced to the form of a hollow seta as in the Diptera, or many-jointed as in Bees. It is frequently fringed by tactile or gustatory bristles and papillæ. When Savigny named it the 'hypopharynx' in the Flies, he entirely overlooked its real nature.

In the more generalised Insecta, although the appendicular portion of the labium, the modified second pair of maxillæ, consists of parts which can be more or less readily recognised as corresponding with the parts of the first pair, they are never so large or complex, and there is a distinct tendency for them to become obsolete in all the more highly modified forms. In the Lepidoptera nothing remains but their palpi, and in the Bees they are reduced to the form of a pair of scales, the paraglossæ, and a pair of long-jointed palps.

The palpi are apparently the last parts which remain in the most highly modified types, and even these are generally regarded as obsolete in the Diptera and Hemiptera—in which, according to received views, the second pair of maxillæ (*labium*) play such an important part in the structure of the suctorial mouth.

**The Maxillæ** (or first pair of maxillæ).—Brullé very carefully figured and compared the maxillæ of numerous insects. I give a copy of some of his figures of the maxillæ and labium of a few well-marked types (Fig. 26). A typical maxilla consists of

a basal joint, the cardo, *c*, which supports the stipes, *s*, or second joint. Three lobes are articulated with the stipes—the first, or external lobe, is usually reduced to a small scale which supports the palpus; it is the palpiger, *p'*. The second lobe, or upper lobe of Kirby, frequently forms a large hood in which the third, or internal, lobe lies when at rest. This second lobe is the galea, *g*. It almost always consists of, at least, two joints, and is usually soft and fleshy. In a few Coleoptera, as the



FIG. 26.—Details of the Maxilla and Labium, after Brullé: 1, maxilla of *Locusta viridissima*; 2, of *Blaps*; 3, of *Pepsis* sp.; 4, of *Xylocopa violacea*; 5, of an Australian species of *Eschna*: *g*, galea; *l*, lacina; *g'*, sous-galea; *s*, stipes; *p'*, palpiger; *c*, cardo; 6, labium of *Copris Isidis*; *l'*, lacina or inner blade of second maxilla; *lig*, ligula; *g'*, outer lobe (galea); *p*, palpus.

Tiger-Beetle (*Cicindela*), the galea is palpiform, and is usually termed the second maxillary palpus [Newport, 9, p. 890]. The third lobe, or lacina, *l*, is frequently a cutting blade, and sometimes has a small claw, the uncus, articulated with it near its extremity. In some phytophagous insects the lacina is converted into an obtuse lobe covered with setæ.

The improbability that so complex a structure can become a mere seta is, to my mind, very great; but when it is

entirely removed from the part of the head to which the maxilla is invariably attached in manducatory insects, it is impossible to admit its homology with that organ. A seta might represent one of the setæ of the lacina, or of the galea, but not the maxilla itself.

The following synonymy will be useful to those who desire to study the maxillæ of insects generally :

**Cardo**, Kirby and Spence. Style, Audouin. Sous-Maxillaire, Brullé.

**Stipes**, Kirby and Spence, Burmeister. Maxilla, Newman. Maxillaire, Brullé.

**Lacina**, Macleay. Stipes, Erichson. Mando, Burmeister. Inter-maxillaire, Straus Durckheim and Brullé.

**Palpiger**, Palpigère, Straus Durckheim, Burmeister and Audouin.

**Galea**, Fabricius. Upper lobe, Kirby and Spence.

**Uncus**, Kirby and Spence. Premaxillaire, Brullé.

#### **b. The Sclerites and Morphology of the Proboscis of the Blow-fly.**

The proboscis of the Blow-fly consists obviously of three parts: a basal portion, the rostrum; an intermediate portion, the haustellum; and a terminal portion, the oral sucker. In the use of the term 'rostrum' I have followed Fabricius; 'haustellum' is also one of his terms, but I have used it in a different sense to that in which he employed it. Kraepelin terms this portion of the organ, with the oral sucker, the true proboscis, but no definite terms have hitherto been applied to the several parts.

The **Rostrum** or basal portion of the proboscis is a membranous cone, attached by its base to the epistome, the genæ, and the pars basilaris of the head-capsule. It supports the haustellum at its apex.

The rostrum is somewhat flattened on its anterior surface, and presents a horse-shoe-shaped sclerite, which forms a hinge on the epistomum, being connected with its oral margin by syndesmosis. I term this sclerite the clypeus. In using the word 'clypeus' in this sense I have followed the nomenclature usually adopted in the Diptera (see page 43). The clypeus articulates with the labrum through the intervention of a tract of syndesmotomic integument, and as Fabricius applied the term to the whole labrum, this use of it is not inappropriate.

The **Clypeus** (Figs. 23, 5 *c*, and 25, *b*) forms the external dorsal portion of the fulcrum, or cephalo-pharyngeal skeleton. This supports the haustellum at its distal extremity.

**The Palpigerous Scales and Palpi.**—On each side of the rostrum, near its apex, there is a convex scale (Pl. VI., *p s*), which supports a single-jointed clavate palpus—the maxillary palpus—at its inner proximal angle. These scales are united in many of the Diptera by a curved plate of chitin, which embraces the posterior surface of the rostrum.

**Sesamoid Sclerites.**—I apply this term to two small nodulated fusiform rods of chitin close to the apex of the rostrum on its

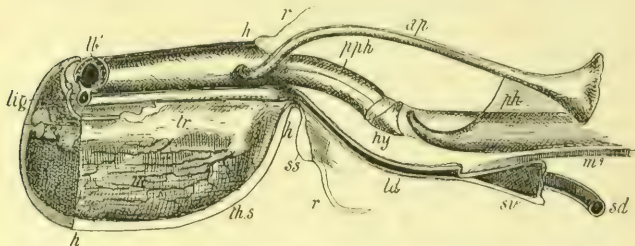


FIG. 27.—A portion of the Proboscis of the Blow-fly, showing the relations of the prelabrum with the theca ligula and pharynx: *ap*, apodème of the labrum; *ph*, the pharynx; *hy*, hyoid sclerite; *pph*, prepharyngeal tube; *rr*, part of the rostrum; *ll'*, the prelabrum; *lig*, the ligula; *h h h*, the haustellum; *ss*, sesamoid sclerite; *th s*, thyroid sclerite; *mm*, muscles; *tr*, trachea; *ld*, lingual, and *sd*, salivary ducts; *sv*, salivary valve.

ventral aspect. They give insertion to the long retractor muscles of the rostrum (Fig. 27, *ss*).

**The Haustellum**, or middle joint of the proboscis, consists of two valves, a large ventral or posterior valve, which I shall term the theca, and a narrow styliform dorsal or anterior valve, the prelabrum.

The prelabrum lies in a groove on the anterior face of the theca, the edges of which overlap it. The theca ends distally in the great two-lobed oral disc, or sucker.

**The Oral Sucker** is a fleshy oval disc, deeply cleft at its anterior

margin. The edges of the cleft are continuous with the margins of the groove in the theca, and are united as far as the edge of the disc by a remarkable bead and channel joint—the thick edge of one lobe of the disc fits into a corresponding cylindrical channel in the other (Fig. 31). The distal surface of the disc is channeled by the well-known 'false tracheæ.' In the centre there is a deep longitudinal fissure, which extends into the tubular mouth situated between the

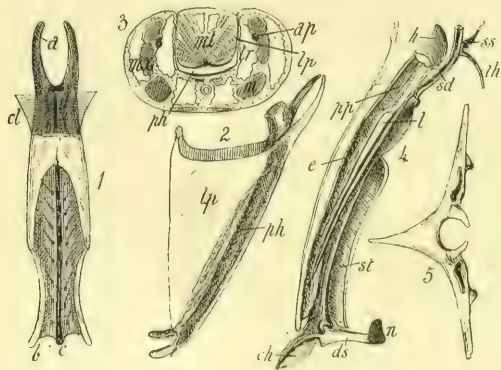


FIG. 28.—1, The fulcrum: *a*, proximal, and *b*, distal cornua; *c*, median raphé; *d*, chitinous plate, uniting the clypeus with the epistome; 2, side view of the same: *ph*, pharyngeal tube; *lp*, lateral plate; 3, transverse section through the rostrum: *ph*, pharynx; *ml*, mesolabrum; *ap*, apodème of the prelabrum; *mx*, maxilla; *m*, muscles; *tr*, tracheæ; 4, a vertical section of the mouth: *h*, hyoid; *pp*, prepharyngeal tube; *e*, inner plate of the prelabrum; *l*, ligula; *sd*, salivary (lingual) duct; *st*, stomal or hypoglossal plate; *ds*, discal sclerite; *n*, nodulus; *ch*, cochleariform sclerite; *ss*, sesamoid sclerite; 5, the furca.

labrum and the theca. The proximal surface of the sucker is convex and covered by setæ; those near its margin are very long and form a fringe.

**Morphology of the Rostrum.**—Transverse sections of the rostrum show that it consists of two parts (Fig. 28, 3), a median anterior or dorsal tube (*ml*), which is continuous with the cavity of the labrum—this represents a mesolabrum, and

a latero-ventral tube (*mx*), which has the same relation to the mesolabrum that the theca has to the prelabrum. In the nymph, at an early stage of development, the separation of the pre- and mesolabrum is not apparent, and the whole lies in a groove, so that the mouth at this period extends back to the epistome; it then very closely resembles the labrum and sheath of the Hemiptera.

Subsequently the fulcrum is developed between the mesolabrum and the grooved part of the rostrum, and the mesolabrum becomes inseparably united with the ventral portion of the rostrum by the fusion of the outer and inner plates of the lateral walls of the fulcrum (Fig. 28, 2 *lp*).

I regard the latero-ventral portion of the rostrum as the basal portion of a pair of united maxillæ; it bears the palpigerous scales and the maxillary palpi. It is probable, however, that part of the thin integument on its posterior or ventral aspect is common to the maxillæ and the rudimentary labium, so that it may be regarded as an extension of the ventral integument between the insertion of the labium and the maxillæ. In the more generalised Insecta (Fig. 22, 4) it is easy to see that the mere obliteration of the deep grooves between the bases of the labium (*mx*<sup>2</sup>) and the maxillæ (*mx*<sup>1</sup>) would result in the formation of a rostrum similar to that of the Blow-fly. Indeed, the fusion of the bases of the maxillæ and labium is far more complete even in the most generalised forms than has hitherto been supposed.

**The Fulcrum**, or cephalo-pharyngeal skeleton (Fig. 28, 1 and 2), has been compared by Kraepelin [70] to a Spanish stirrup-iron with a double foot-plate. It may be described as consisting of a flattened tube, the pharyngeal tube, formed by two pharyngeal plates, a dorsal or anterior, *epipharynx*, and a ventral or posterior plate, *hypopharynx*. The epipharyngeal plate exhibits a strong median raphé, which projects into the pharynx. A pair of horns, cornua (*a*, *b*), project at either end of the pharyngeal tube, and give insertion to several muscles.

On either side of the pharyngeal tube there is a somewhat triangular lateral plate (*lp*), formed by the adjacent walls of the

mesolabrum and the base of the maxillæ. This plate consists of two laminae towards the pharynx, but the two are inseparably united throughout the greater part of its extent. The anterior or dermal edges of the lateral plates of the fulcrum are continuous with the clypeus, so that the mesolabrum is bounded by the clypeus, the lateral plates of the fulcrum, and the epipharyngeal plate; it contains the dilator muscle of the pharynx, which, by withdrawing the epipharyngeal from the hypopharyngeal plate, draws fluid through the tubular mouth into the pharynx, so that the fulcrum is a powerful instrument of suction. It also forms a movable support for the whole haustellum.

**Morphology of the Fulcrum.**—Gerstfeldt [55] is, I believe, the only author who has anticipated me in the statement that the maxillæ enter into the composition of the fulcrum, but he merely observes, 'The anterior lancet (labrum) shows distinctly, by the presence of a median raphé, that it is formed of two halves, which must be the blades of the maxillæ (*Kieferladen*). They rest upon a piece extending backwards (the fulcrum), which appears to be the united stipites, from which two slender, nail-shaped parts diverge downwards and backwards. These Straus termed glosso-pharyngeal apophyses in *Melolontha*, they are analogous with the cardines' [55, p. 25]. I so far agree with Gerstfeldt as to regard the outer portion of the lateral plate of the fulcrum as a portion of the stipes of the maxilla. His other statement, that the nail-shaped processes represent the cardines, is undoubtedly incorrect, and the fusion of the blades of the maxillæ with the labrum is by no means proved. Although I formerly held this view myself, I now think it far more probable that the lacinæ are undeveloped in all those flies in which only two median lancets exist. The lacinæ of the maxillæ are present, however, when paired lancets enter into the composition of the mouth armature, as in the *Tabanidæ*.

Menzbier [50] states that the fulcrum is developed in the chitinous lining of the stomodæum, and regards it as an internal organ. This view is inconsistent with its developmental history

and its connection with the clypeus. It has, however, been very generally adopted.

**Retraction and Extension of the Proboscis.**—The proboscis is an erectile organ. It is flaccid and folded on itself when not in use, but is capable of being rendered rigid by the injection of air into the extensive tracheal sacs which lie in its cavities. When at rest the only rigid parts are the fulcrum, the prelabrum and the theca. The two lateral halves of the flaccid stomal disc are folded together, so that the stomal surface is concealed. The disc is also flexed on the ventral surface of the theca. The haustellum is folded forward on the rostrum, so that the back of the labrum lies against the clypeus, and the fulcrum turns upon the epistome, so that its dorsal surface looks downwards and backwards. In this position it lies entirely within the head capsule, and the maxillary palpi rest one on either side of the haustellum, which is also more or less completely withdrawn into the head capsule. The thin integument of the ventral surface of the rostrum is invaginated into itself, and lies in folds above and behind the retracted proboscis.

When the proboscis is in use, it is projected from the head capsule, and rendered stiff by the injection of air into its tracheæ. Its varied movements are brought about by the action of muscles; the flaccid proboscis is also folded and withdrawn into the head capsule by means of retractor muscles. The nature and precise mechanism of the movements of the proboscis will be further discussed in another section.

**The Prelabrum** is the rostellum of Fabricius, the labrum-epipharynx of Menzbier and most recent authors. It is a hollow prolongation of the mesolabrum, and lies in the groove of the theca. It exhibits two pairs of sclerites, one pair on its dorsal convex surface and one pair on its oral concave surface; the latter form the roof of the long tubular mouth. These sclerites are all fused in the fully-developed imago, but the two dorsal are readily separated from the two oral sclerites in the young imago, and also in the skeletons of mature insects prepared with caustic soda or potash.

The separation of the sclerites forming the upper and lower surface of the labrum gave rise to the view that one pair represent the labrum and the other the epipharynx. As the labrum does not consist of a single plate in any insect, but is always a hollow process, this is not a tenable view (Kraepelin [70]).

The external (dorsal) pair of sclerites are fused together at their proximal extremity, where they articulate with a pair of

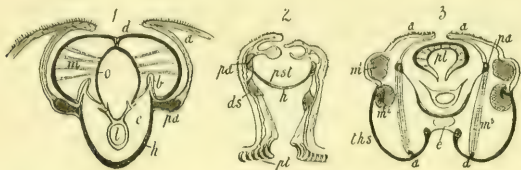


FIG. 29.—1, A section through the mouth in the plane a little below that marked by the line *pl*, Plate VI.: *m*, cavity of the prelabrum containing muscles; *a*, edges of the groove in the theca; *d*, dorsal, and *o*, oral sclerites; *l*, the ligula and salivary duct; *b*, the hypoglossa, and *pa*, the paraphysis. The cavity *c* is cut off from the alimentary tube when the ligula is brought into contact with the labrum; it is indicated by the letters *st* in Plate VI. 2, A section through the anterior dorsal edge of the oral sucker, showing the dislocated bead and furrow which closes the prestomum and the lower edge of the hypoglossa; the lips are strongly flexed on the theca: *h*, hypoglossa; *pa*, paraphysis; *ds*, discal sclerite; *pl*, pseudotracheæ; *pst*, prestomum. 3, A section through the haustellum near the plane *sg* in Plate VI.: *pl*, prelabrum; *lks*, thyroid shield; *m*<sup>1</sup> to *m*<sup>3</sup>, muscles in the cavity of the theca; *e*, elastic band. The ligula is seen between the hypoglossa and the prelabrum.

apodèmes—the glosso-pharyngeal apophyses of Straus Durckheim already referred to (Fig. 27, *ap*). These lie in the cavity of the rostrum, and are the 'nail-like pieces' which Gerstfeldt thought analogous to the cardines of the maxillæ.

As the cardines of the maxillæ represent the hollow basal joint of a ventral appendage, no possible modification of them could produce a mere internal apodème; and, further, the cutaneous attachment of these apodèmes in front of the palpi-gerous scale entirely precludes such a view of their nature. Menzbier, I think correctly, regards them as simple muscle tendons [50, p. 65].

The sclerites, of the under surface of the labrum, form a complete tube, the prepharyngeal tube (Fig. 28, *4*, *pp*), by uniting with the base of the ligula. By means of this tube the mouth communicates with the pharyngeal section of the alimentary canal. It curves towards the ventral surface of the proboscis.

**The Pseudolabium.**—As that part of the haustellum which I have called the theca, together with the oral sucker, is a morphologically distinct part, it will be convenient to adopt a term for its designation. As has been already observed, it is usually regarded as the labium, or lower lip. It forms the floor of the mouth, is connected on its oral surface with the root of the tongue, and terminates in a pair of lobes united behind—the oral sucker; these lobes have been alternately regarded as modified palpi and paraglossæ. Although functionally a lower lip, its manner of development and its relation to the rostrum show that it is not a labium, and that it is not developed from the second pair of maxillæ, therefore I propose the term ‘pseudo-labium.’

The greater part of the labium of a generalised insect consists of the galeæ of the second pair of maxillæ. My contention is that, in the flies, the second pair of maxillæ are exceedingly rudimentary or entirely absent, and that their place is taken by the first pair, the united galeæ of which form the pseudo-labium.

**The Sclerites of the Pseudolabium.**—I have been unable to find any names for these sclerites, in published works, which are suitable for their designation; I am therefore obliged to suggest the following new terms:

I term the large ventral sclerite of the theca (Fig. 30, *4*), the ‘thyroid’ from its form. It articulates at its distal extremity with the ‘furca,’ by which name I distinguish Kraepelin’s ‘Untere Chitingabel’ (Fig. 28, *5*).

The oral sclerites of the theca are three in number. They lie in the groove which forms the mouth cavity; a median sclerite, the hypoglossa (Fig. 28, *st*), and two lateral rods, the paraphyses (Pl. VI., *pa*), one on each side of the hypoglossa.

The distal ends of the paraphyses articulate with a pair of

plates (Fig. 28, 4, *ds*), discal plates the 'Obere Chitingabel' of Kraepelin, which support the pseudotracheæ and the teeth.

The **Thyroid** is a shield-like convex plate which covers the whole of the ventral and lateral surfaces of the theca (Fig. 30, 4). It terminates distally in a pair of divergent processes, or cornua; these articulate with grooves in the furca (Fig. 28, 5). Its lateral margins are strengthened by two strong internal ridges which terminate in the cornua (Fig. 30, 4, *f*). The thyroid is developed after the insect emerges from the pupa, only its cornua are already present in the very young imago.

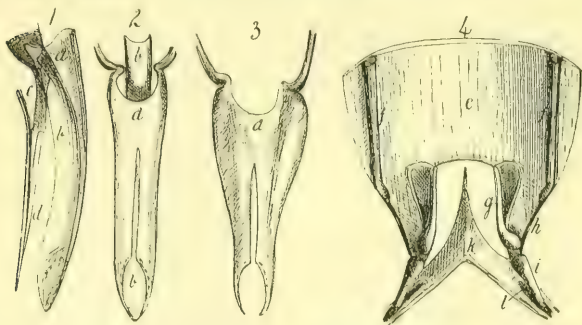


FIG. 30.—Details of the haustellum: 1, the prelabrum and ligula: *a*, external, and *b*, internal plate, the labrum and epipharynx of Menzbier; *c*, part of the prepharyngeal tube; *d*, the ligula; 2, the prelabrum seen from in front; 3, the external plate, labrum of Menzbier; 4, part of the thyroid sclerite: *c*, body of the sclerite; *f*, lateral ridges; *g*, inner, and *h*, outer supports of the cornu; *i*, the cornu; *k*, the furca; *l*, groove in which the cornu is lodged.

In the well-known preparations made by the late Mr. Topping, the thyroid shield is undeveloped, and the preparations exhibit other evidences of having been made from flies almost immediately after their escape from the pupa. The facial sclerites and the epistome are undeveloped; the furca has also been cut through in the middle line, probably with a pair of scissors with very small strongly-curved blades—or by a V-shaped incision made close to the junction of the theca and the

oral lobes. Gerstfeldt and Menzbier follow Kirby and Spence, and term the thyroid the mentum.

The **Furca** (Fig. 28, *f*) is situated on the back of the oral sucker; it presents a triangular plate, the angles of which are processes prolonged to the edges of the disc. The posterior process is short and slender, the lateral processes are very strong, and each exhibits an elongated fossa near its origin, which articulates with the corresponding cornu of the thyroid.

When the oral sucker is closed, the lateral processes of the furca are parallel with each other, and appear to be mere continuations of the thyroid cornua. When the disc is expanded these processes lie in the same plane, or are even bent back at an obtuse angle by the action of a pair of powerful muscles inserted into them. When the disc is expanded the thyroid cornua are bent back and slide outwards in the grooves in the furca. The closure of the disc is due to the elasticity of the thyroid cornua, which act on the furca like a pair of springs.

The **Epifurca**.—I apply this term to a slender rod of chitin (Pl. VI., *ep f*), near the margin of the posterior surface of the disc, the axis of which is at right angles with the lateral process of the furca.

The **Hypoglossa** or stomal plate (Fig. 28, *st*) is a thin, gutter-like plate which forms the floor of the groove in the theca. It does not extend as far back as the base of the ligula, and terminates at its distal end in a thin sharp-pointed edge, which projects between the lateral lobes of the stomal disc.

The **Paraphyses** (Pl. VI., *pa*), are regarded by Kraepelin as the thickened edges of the plate I have termed the hypoglossa. In the young imago they are distinct rod-like sclerites. The distal ends of the paraphyses exhibit articular surfaces, which form a kind of hinge-joint with the discal sclerites.

The **Discal Sclerites** (Fig. 28, *ds*) lie deeply in the cleft between the two lateral halves of the oral disc. I shall term this cleft the prestomum. The discal sclerites form the upper chitinous fork of Kraepelin.

Each discal sclerite consists of a quadrilateral elongated

plate, the body, and of a process at its dorsal extremity. This process is an elongated spoon-shaped scale, hence I shall term it the 'cochleariform process'; but in profile it appears like a curved hook (Fig. 28, *4, ch*). The distal margin of the body of the sclerite supports a number of chitinous folds, and a treble row of bifid rods, the teeth of the prestomum. The chitinous folds form the inner orifices of the pseudotracheæ and the lateral walls of the prestomum (Fig. 31).

The ventral extremities of the bodies of the discal sclerites are united by a thick nodule of black chitin, the nodulus (Fig. 28, *4, n*). The nodulus is connected with the furca by a strong elastic ligament.

The proximal margin of the discal sclerites is attached by a loose syndesmotomic cuticle with the distal end of the hypoglossa. This cuticle forms a deep pouch. I shall term the pouch the 'poculum' (Fig. 31, *p*). The anterior proximal angle of the body of the discal sclerite articulates with the end of the paraphysis.

The discal sclerites are parallel with each other when the oral disc is flaccid and folded, and they are then flexed on the paraphyses, so that the angle between the discal sclerite and the paraphysis is acute.

When the prestomum is open the paraphyses are separated, and the discal sclerites diverge in front, and form a more obtuse angle with the paraphyses. In this position the orifice of the poculum is triangular, and the ligament between the nodulus and the furca is stretched.

The distal surface of the oral disc exhibits two lateral halves, separated by a deep fissure, the prestomum, which may appear as a mere median cleft when it is closed, or as a deep fossa when open.

Under slight violence the union between the two edges of the pseudolabium, which extends from the dorsal margin of the stomal disc to the junction of the middle and distal third of the prelabrum, is ruptured. The bead in the left is drawn from the furrow in the right edge, and the disc appears cordiform instead of oval. The prestomum opens by this cleft on the

dorsal and proximal surface of the disc, and the two lips lie flat, the walls of the prestomum being thrown into the same plane as the surface of the disc.

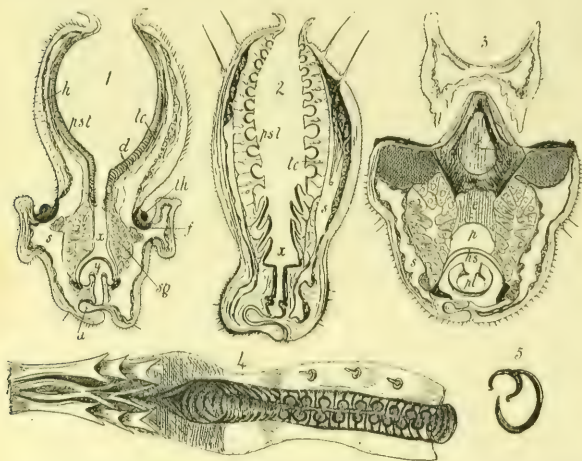


FIG. 31.—Details of the Oral Sucker: 1, A section through the disc just in front of the prelabrum: *x*, cavity of the prestomum; *y*, cavity of the mouth; *a*, dorsal seam formed by a bead and furrow; *sg*, labial salivary gland; *d*, duct; *th*, thyroid cornu; *f*, furca; *tc*, tendinous cord; *s*, cavity; *h*, hypoderm cells. 2, A similar section in a more anterior plane passing across the pseudotracheæ: *x*, prestomal cavity and the bases of the teeth; *tc*, tendinous cords; *psl*, pseudotracheæ. 3, A section through the junction of the theca and the oral sucker: *f*, furca; *e*, elastic ligament; *p*, poculum, with labial glands on either side; *hs*, hypoglossal sclerite; *pl*, extremity of the prelabrum. 4, A pseudotracheal vessel and the prestomal teeth and folds. 5, An isolated ring of one of the pseudotracheæ.

The distal surface of the disc may therefore be described as consisting of two parts, the prestomal and the discal.

The prestomal portion is formed by the discal sclerites and the teeth and folds of the prestomum (Fig. 31, 4) with the inner orifices of the pseudotracheæ between them.

The **Pseudotracheæ** are cylindrical channels on the oral surface of the disc. These channels are sunk more or less deeply in the disc, according to the degree of its inflation. When the disc is fully inflated they open by zigzag, longitudinal fissures on its oral surface.

The channels of the pseudotracheæ are kept open by elastic chitinous rings, which somewhat resemble the rings in the tracheal vessels, hence the name pseudotracheæ.

The pseudotracheæ vary in number from twenty-eight to thirty-two pairs. They may be described as forming three sets. The seven anterior on each side unite and form a single trunk, which opens into the prestomum between the first and second teeth. Ten to twelve intermediate pseudotracheæ run straight from the margin of the disc directly into the prestomum. The remainder unite and form a trunk, which runs nearly parallel to its fellow, and opens into the prestomum at its shallow ventral extremity.

The **Teeth** (Fig. 31) are oblong plates of chitin, bifid at their free extremities. There are three rows of teeth on each side of the prestomum. The teeth of the innermost row are free, except at their bases, which are connected with the lateral plate of the discal sclerite. The intermediate teeth are only free one-third, and the outermost one-sixth, of their length.

The free margin of each tooth near its junction with the discal sclerite is thickened, and is continued as a ridge, which diverges from the base of the tooth on the chitinous wall of the prestomum.

These ridges are parallel with each other and with the margins of the openings of the pseudotracheæ, the rings of which appear to be of the same nature as the ridges supporting the teeth (Kraepelin [70]).

The teeth of the inner row are much stronger and thicker than those of the outer rows, and they lie in the grooves between the ridges which support the intermediate row of teeth. The arrangement will be best understood by the accompanying figure (Fig. 31), or by a study of the proboscis itself.

The details of the structure of the pseudotracheæ and of the

integument of the proboscis will be more fully considered in another section of this work.

**The Ligula** (hypopharynx) is the only lancet-like mouth organ in the Muscidæ. It is situated in the groove of the pseudolabrum, and arises from its proximal end.

It consists of a prolongation of the salivary (lingual) duct, and in transverse sections, through the middle region of the labrum and theca, the ligula exhibits a flange-like projection on either side, which articulates with a groove in the side of the labrum, so that the tube through which the food passes is formed entirely by the ligula and the labrum (Fig. 29).

Further back the two flanges unite on the dorsal surface of the salivary tube, and the latter becomes separated from the plate produced by the union of the flanges. This plate is concave towards the mouth, and its edges unite with the edges of the oral sclerites of the labrum and surround the posterior or proximal portion of the mouth. This I term the 'prepharyngeal tube.' Kraepelin names the distal end of the prepharyngeal tube 'the true mouth orifice.' The labrum, or upper lip, projects from it dorsally, and the ligula is a prolongation of its ventral margin.

If my contention is correct, *that the proboscis consists mainly of the first pair of maxillæ*, the true labium would lie at the base of the ligula, and form the lower boundary of the true mouth orifice. I think it probable that the flanges are the rudiments of the paraglossæ.

In the larva (Fig. 7) I have already shown that the true mouth lies between the labrum and the ligula, and is concealed by the great maxillæ. The flanges on the ligula of the imago originate from two rows of cells, which first appear in the root of the ligula in the larva, and lie in a true labium developed from the second pair of maxillæ (Fig. 5, *lb*). In Fig. 6 it is easy to see that a retraction of the ligula (*l*) and a great enlargement of the maxillæ (*mx*) would give rise to a condition similar to that seen in the fly larva, and precisely the same relations appear to exist in the imago of the true flies and in the Diptera generally.

**The Hyoid Sclerite** (Fig. 28, *h*). The last sclerite which I have to describe in the proboscis of the Blow-fly I term the hyoid. It is developed in the wall of the alimentary tube, between its pre-pharyngeal portion and the pharynx. It is U-shaped, with its convexity backwards, and it keeps this section of the alimentary tube open when the haustellum is flexed on the rostrum.

### c. The Proboscis of the Immature Imago.

When the imago first emerges from the pupa case, the proboscis is immovable, and lies on the ventral surface of the thorax between the legs, like the proboscis of an hemipterous insect.

The rostrum at this period consists of two very distinct parts, a proximal portion in front of, and a distal portion behind, the insertion of the palpi.

The proximal portion of the rostrum (Fig. 25, *a b*) closes the peristomal cleft of the head capsule, and consists of a central part, the epistome clypeus and metalabrum, and of two lateral parts, the maxillary folds (Mihi). The maxillary folds are separated from the metalabrum by two deep inflections of the integument, which form the lateral plates of the fulcrum.

The distal portion consists of the mesolabrum, continuous with the metalabrum, and of two large sub-cylindrical palpi-gers, covering and concealing a portion of the theca (Fig. 25).

The prelabrum is seen at the distal extremity of the mesolabrum, and lies chiefly upon the lobes of the oral sucker. Between these lobes and the theca there is a distinct ovoid swelling, from the wall of which the body of the furca is developed. I shall term this ovoid swelling the 'discophore' (Figs. 25, *d* and 32). A second smaller swelling intervenes between the pre- and mesolabrum; it is apparently nothing more than a protuberance of the syndesmosis at the base of the prelabrum.

The ventral (at this period upper) surface of the proboscis is much shortened by two deep infoldings of the rostrum, whilst

the dorsal surface is lengthened by the elongation of the mesolabrum and the palpigerous scales. The oral lobes are also proportionately longer than at a later period.

At a still earlier period of development in the nymph (Fig. 32), the labrum is less displaced in relation to the theca than in the newly-escaped imago. The head is then smaller, and it is apparently the unequal growth of the head which pushes the labrum towards the distal extremity of the proboscis.

During the evolution of the proboscis, after the escape of the imago from the pupa, the ventral (upper) surface of the proboscis is gradually elongated, and the discophore is converted into a portion of the dorsal surface of the oral sucker, whilst the

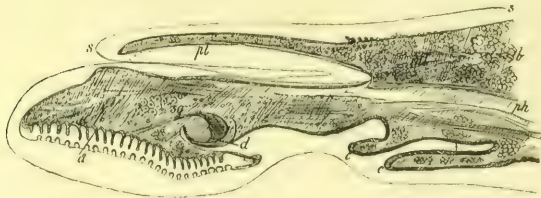


FIG. 32.—A longitudinal median section of the proboscis of a nymph, about the middle of the second week : *a*, boundary of air space between the hypodermis and the pseudotracheæ of the disc ; *b*, aggregations of embryonic cells ; *c c*, folds of the rostrum ; *d*, the discophore ; *p h*, the pharynx ; *m l*, the meso- and *p l*, the prelabrum ; *s g*, labial gland ; *s s*, the sheath.

theca assumes its position above the labrum. At the same time the cylindrical portion of the rostrum becomes shortened and conical, whilst the proximal part is converted into a membranous cone.

#### d. The Comparative Anatomy of the Proboscis in the Diptera.

The form of the proboscis in the immature imago of the Blow-fly affords an easy transition between the most diverse types of the dipterous mouth. The various modifications of

the proboscis appear to depend on the greater or less development of the several parts which can be recognised in the immature Blow-fly, with the presence or absence of paired lancets, which do not appear at any stage of development in the Muscidæ.

The position of the palpi, which are always present, has been too much neglected in the comparative study of the mouth organs of the Diptera—just as the position of the antennæ has, in the study of the head capsule. In the Tipulidæ the palpi are near the extremity of the proboscis, and the greater part of the organ corresponds with the rostrum, whilst in the Tabanidæ and the Gnats (Culicidæ) they arise close to its base, the rostrum being exceedingly small or entirely absent. The parts developed from the discophore may be very large, whilst the theca is rudimentary; or the discophore may, as in the flies, become a portion of the dorsum of the oral sucker, so that it is apparently absent.

**The Maxillary Palpi** are usually three or four jointed. In the Muscidæ, however, there is never more than a single joint. These palpi, in the Diptera with paired lancets, usually form a sheath for them, as in the Tabanidæ.

**The Rostrum** is very generally highly chitinized, and forms a kind of beak covering a fulcrum very similar to that of the fly. In such cases the proboscis is incapable of being withdrawn into the head capsule—sometimes, as in *Bombylius*, the rostrum is very short, and the fulcrum is then rudimentary.

**The Prelabrum** is always a prolongation of the dorsal portion of the rostrum, with which it articulates; but it is usually free, and does not articulate with the ligula, so that it can be lifted from the groove in the pseudolabium.

**The Pseudolabium** can generally be folded back as far as the base of the palpigerous scales to which it is always attached.

In the Crane-flies (*Tipulidæ*), however, it is very short and encloses the labrum, as in the true flies. In *Bombylius* it is of extraordinary length. The oral sucker varies greatly in form, but in the Crane-flies it so closely resembles a galea formed of two joints that it is difficult to understand why it has so long been

regarded as a labium. It is articulated by syndesmosis with the palpigerous scales, and there is no thyroid sclerite, but both a furca and a discal sclerite are present. The furca is articulated with an internal sclerite, probably the body of the furca invaginated, and the discal sclerite is supported by two short, broad paraphyses, which articulate with the edges of the labrum.

**Paired Lancets.**—One of the most marked characters in the Blow-fly and all the Muscidæ is the absence of paired lancets. Two pairs of these are always present in the predaceous flies, and a single rudimentary pair have been detected in some of the Syrphidæ. When two pairs of lancets are present, they are similar to the two pairs of bristles found in the Hemiptera. These have been named mandibles and maxillæ in both orders, but on very insufficient evidence.

So far as I know, there is no dipterous or hemipterous insect in which there are any traces of mandibles, and the parts so named are always a part of the maxillæ, and articulate with the palpigerous scale. Dimmock [68, p. 28] identifies the parts which Menzbier supposed to be mandibles in *Syrphus*, with the maxillæ.

**The Mouth Armature of the Pulicidæ.**—The structure of the mouth in the Fleas (*Pulicidæ*) is of extreme interest in relation to that of the Diptera, as it is manifestly intermediate in character between the dipterous and the hemipterous mouth. As long ago as 1749 Rösel\* recognised the affinity of the Fleas with the Diptera, a view also adopted by Straus Durckheim and Oken,† and one which has been recently widely accepted. Macleay‡ perceived the intermediate relation of these insects with the Hemiptera, on the one hand, and the Diptera on the other.

In the Fleas the palpiger (Fig. 33), which has frequently been mistaken for a mandible, is a large triangular hollow blade with trenchant edges. It supports a four-jointed palp near its proximal margin.

\* Rösel, 'Insektenbelustigungen,' 1749.

† Oken, 'Naturgeschichte für Schülen,' p. 775. 1821.

‡ Macleay, 'Horæ Entomologicæ,' i., p. 357. Lond., 1821.

This palp has frequently been mistaken for the antenna. The true antenna is three-jointed, with a large terminal joint, closely resembling that in the Muscidæ. It lies in a groove behind the simple eye. This position of the antenna is a clear indication that the simple eye in the Fleas is not homologous with the great compound eyes of insects, which are never in front of the antennæ. Its situation at the root of the palpigerous blade of the maxilla apparently shows that it is more nearly related to the maxillary eye-like organs of the fly larva (see page 71).

The inner proximal edge of the palpiger consists of a strong sclerite (Fig. 33, *a a*), which articulates with a socket in the peristome below and supports the lacina above. It is the hinge of the maxilla, and it gives off a curved process (*g*) in front, to which the margin of the sheath or pseudolabium is attached.

The pseudolabium frequently resembles and has been described as a pair of palpi. This arises from the great transparency of the ventral part of the organ. When properly separated and prepared, the nature of the part is unequivocal, and it agrees in every detail with the four-jointed sheath of the hemipterous mouth. I regard this sheath as formed by the united galeæ of the maxilla. I have already drawn attention to the palpiform character of the galea in *Cicindela*, so that the resemblance of this sheath to a pair of united palpi, similar to the labial palpi of the Hymenoptera, cannot be a valid argument in favour of its being formed by the union of a pair of labial palps; and its connection with the base of the maxilla indicates sufficiently its true character.

Between the hinge sclerites of the maxillæ a median prolongation of the peristome (Fig. 33, *b*) supports the curious tubular ligula; these are the only representatives of the lower lip—labium—and the labrum as a distinct projection of the peristome is entirely absent in all the Pulicidæ.

Great differences of opinion exist as to the nature of the mouth organs in these remarkable insects. Taschenberg,\* the

\* Taschenberg, Otto, 'Die Flöhe,' 8vo, Halle. 1880.

latest writer on the subject, says the plates which support the palpi are maxillæ, and the lancets, my lacinæ, are mandibles. For further information on the views held by various authors,

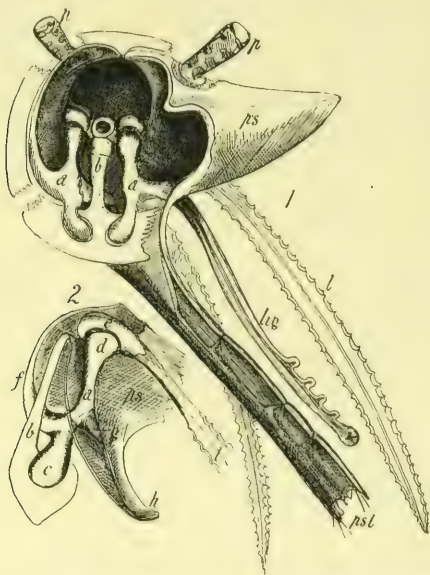


FIG. 33.—1, The trophi of a Flea removed from the head and seen from behind : *a a*, hinge of the maxillæ ; *b*, support of the ligula ; *p p*, palpi ; *ps*, palpigerous scale ; *l*, lacinia ; *lig*, ligula ; *psl*, pseudolabium. 2, A portion of the same, seen from its inner side : *g*, process of the hinge supporting the pseudolabium ; *c*, articulation with the peristome ; *f*, process of the hinge which strengthens the palpigerous scale ; *d*, articular head supporting the lacinia ; *e*, articular extremity of the lacinia ; *h*, the base of the pseudolabium cut through ; the other letters as in 1.

which are exceedingly confused and conflicting, I must refer my reader to Taschenberg and Gerstfeldt [55].

That both pairs of setæ in the Diptera are parts of the

maxillæ is sufficiently obvious in *Tabanus*, where they are supported by a massive hollow cardo, or basal joint, and also in the curious sand-fly (*Simula reptans*), one of the *Biblionidæ*, the female of which is a ferocious blood-sucker. In these insects the palpiger bears a broad trenchant blade, and the lacina is strong and serrated as in the Fleas.

Synonymy of the mouth organs of the *Diptera*; the following are the most important :

**Rostrum**, Fab. Kopfkegel, Kraepelin. Russelstiel, Graber.

**Labrum**, Clypeus, Fabricius. Properly prelabrum, Mihi. Operculum, Mihi [62]. Labrum of authors generally. Labrum-epipharynx, Menzbier.

**Fulcrum**, Menzbier and Dimmock. Pharynx, Meinert.

**Palpiger**, Mihi. Mandible. Superior lancet.

**Lacina**, Mihi. Inferior lancet. Maxilla.

**Palpus**, Maxillary palpus, Kirby and Spence, Gervais. Labial palpi in some *Diptera*. Savigny.

**Ligula**, Hypopharynx, Savigny.

**Pseudolabium**, Mihi. Labium, Savigny, and generally.

**Oral Disc**, Mihi. Labial palpi, Burmeister, Erichson and Kraepelin.

The other parts mentioned in the above description have not hitherto received names except where the synonymy has been already indicated.

#### 4. THE THORACIC EXO-SKELETON.

##### a. General Morphology.

The Thoracic Exo-skeleton exhibits great uniformity, even in the most dissimilar insects. It always consists of three highly modified somites, which Audouin [38] named the pro-, meso-,

##### Bibliography :—

72. JURINE, L., 'Observations sur les ailes des Hymenopteres.' Mém. Acad. Sc., Turin, xxiv., 1820. 4to.
73. CHABRIER, J., 'Essai sur le vol des Insectes.' Mém. du Museum, tom. vi. to viii., 1820-22. Paris, 4to.

and metathorax, to which the first abdominal somite, Latreille's segment médiaire, is added in many of the Hymenoptera.

The nomenclature of the several sclerites which form the walls of these somites is still unsatisfactory and confused. This has arisen partly from the difficulty of defining the limits of the somites, but chiefly from an attempt to make the three somites conform to an ideal type which originated in the mind of Audouin [38 and 39]. Audouin examined the meso- and metathorax in a great number of insects, and found the same parts represented, more or less distinctly, in all; and there is no doubt that the meso- and metathorax, when each has a pair of wings, exhibit a close resemblance to each other. The attempt, however, to identify the sclerites of one with the other is not always successful, and when this process is extended to the prothorax it leads to nothing but confusion.

Audouin took the most highly-modified wing-bearing segments as his type, and expected to find the same structures in the less highly-modified wingless prothorax. Instead of deriving the more specialised from the more generalised, he set up an ideal highly specialised type and attempted to make the less specialised somites of the body conform to his ideal.

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74. LATREILLE, P. A., 'De quelques Appendices Particuliers du thorax de divers Insectes.' Mém. du Museum, tom. vii., 1821.
  75. MACLEAY, 'An Explanation of the Comparative Anatomy of the Thorax of Winged Insects, with a review of the present state of the Nomenclature of its parts.' Zool. Journ., vol. v., p. 145, 1830.
  76. SCHIÖDTE, J. C., 'Bidrag til Kundskab om Insekternes Thorax, med fortrinligt Hensyn til Latreille's Theoric om Segment médiaire og til Forekomsten og Fordelingen af Spiracula Thoracica.' Overs. Danske Vidensk. Selskabs Forhandlinger, 1856, p. 135. An English résumé in Ann. Nat. Hist., ser. iii., vol. xv., p. 483.
  77. LOEW, HERMAN, 'Monograph on N. American Diptera,' vol. i., 1886.
  78. HAMMOND, A., 'On the Thorax of the Blow-fly.' Journ. Linn. Soc. Zool., vol. xv., 1879.
  79. GOSCH, C. C. A., 'On Latreille's Theory of "le Segment Médiaire"' (in English). Schiödte Nat. Tidsskr., Række iii., Bd. xiii., 1881-83.
  80. BRAUER, F., 'Ueber das Segment Médiaire Latreilles.' Sitzungb. Akad., Wien., Bd. 85, 1882.
  81. OSTEN-SACKEN, C. R., 'An Essay on Comparative Chætotaxy.' Trans. Entom. Soc., Lond., 1884. Originally published in Mitth. der Münchener Ent. Ver., vol. v., 1881.

Audouin's own words, when translated, are: 'If we wish to study the anatomy of an insect's thorax, we ought, after dividing it into three segments, to seek for a sternum on the inferior surface of each; for an episternum, a parapteron, and an epimeron on the flank. We should also search for an entothorax, a peritreme, and a trochantin. I say that we should seek for them, not that we should find all these in each insect; very generally their union is so complete and intimate that they cannot be demonstrated, but as in other cases these pieces are present, it is more rational to conclude that the same material is utilised in all than to suppose new creations are perpetually occurring' [39, p. 126]. Audouin's ideal segment of the exo-skeleton has been generally adopted as typical; and each segment of the thorax is said to consist of a sternum, two lateral plates, the episternum in front and the epimeron behind united by an oblique internal ridge, and of four dorsal plates, one in front of the other, named respectively the prescutum, the scutum, the scutellum, and the post-scutellum.

The united episternum and epimeron are also termed the pleuron, and the four dorsal plates form the tergum—hence a segment is described as consisting of a dorsal arch, the tergum, a ventral arch, the sternum, and of a pair of pleura between the dorsal and ventral arches.

The term 'pleuron' has been unfortunately applied in quite a different sense in the Crustacea—in these it means a lateral prolongation of the dorsal arch, which forms the gill cover in the decapods. By the rule of priority the term should certainly be used as Audouin used it; I shall therefore call the united episternum and epimeron the pleuron, and suggest that the pleuron of the Crustacea should be called the epipleuron.

In the prothorax a sternum and a pleuron are still recognisable, but it is doubtful, I think, how far these correspond with the same parts in the meso- and metathorax. There is usually a dorsal arch formed of one or more sclerites in all three thoracic somites, but sometimes this is reduced to a mere rim, and the homologies of the several dorsal plates of the meso- and metathorax are all exceedingly doubtful.

Audouin's ideal segment in its simplest form represents the type of a wing-bearing somite, but if we seek the more primitive condition, it must be amongst terrestrial forms in which the skeletal ring in each somite consists of a dorsal and ventral arch, each developed from two lateral halves.

Macleay [75] supposed that each thoracic segment consists of four united sub-segmental annuli, but, so far as I can see, this view is entirely unsupported by facts, and the whole evidence of development is adverse to it.

Another, and perhaps more tenable, view is held by Patten [48]. He regards each segment as the result of the fusion of two primary somites or metameres. This hypothesis originated from the fact that the ventral lateral appendages of the somites are frequently bifurcate, or consist of an exo- and an endopodite, in the more generalised Arthropoda, a character which persists in the maxillæ of insects, and, as I have already observed, and shall show hereafter, also in the thoracic legs of the fly at an early period of development.

In support of his hypothesis, Patten [48] makes the following statements :

1. 'In Scolopendra each neuromere, or pair of segmental ventral ganglia, has four pairs of nerves, two probably motor and two sensory ; and in all arthropods, the neuromeres of which have been carefully studied, each exhibits two transverse commissures.

2. 'In *Acilius* each segment has two pairs of tracheal openings, spiracles, one pair easily seen near its anterior margin, and one pair very rudimentary and difficult to recognise near its posterior edge.

3. 'The double character of the segments of *Julus* is evidenced according to Heathcote by the duplication in each segment of the cardiac ostia, arteries, neuromeres, tracheæ, and legs ; whilst in *Scorpio* the neuromeres present a distinctly double character.'

Whilst admitting the apparent validity of Patten's arguments, I would observe, however, that his hypothesis is not supported by developmental evidence, so far as the Insecta are concerned,

and the three thoracic segments are always represented by three metameres, both in the larva and in the embryo. Although a ventral groove appears in the somites of the abdomen in the larva of the Muscidæ (see Fig. 4, *a* and *d*), nevertheless, each thoracic segment in the imago is developed from two pairs of imaginal discs only.

I am also unable to see that the structure of the thorax of the imago is more easy of interpretation by the assumption that each segment consists of two united rings. Yet I cannot regard the supposition as unsupported, although I am unable to accept it as proven.

**The Ventral Appendages** of the thorax, or legs, are divided into a series of joints or segments. The basal joint is known as the coxa, or hip; the second is the femur, or thigh\*; the third the tibia, or shank; and the terminal joints, usually five in number, form the tarsus, or foot.

The bifurcate form of the ventral appendages already alluded to appears to be a common phenomenon in all the more generalised forms of arthropods. At first sight, although apparent enough in the maxillæ, this condition seems to be entirely absent in the thoracic legs of insects. It is usual to consider that one of the divisions of the limb, that corresponding with the exopodite in the Crustacea, is suppressed.

During the evolution of the thoracic limbs, in the imago of the Blow-fly, from the lower thoracic imaginal discs, they are, however, bifurcate in what I shall term the third stage of development. At this stage the coxa, femur, and tibia are represented by an elongated sac (Fig. 34, *2*, and *3*, *ex*), which is united at its open extremity with both the thoracic wall and the five-jointed tarsus. A longitudinal septum and two constrictions afterwards appear and separate the femur and tibia. It would seem, therefore, that the femur and tibia are developed from the outer limb of a bifurcated appendage, and the coxa forms a basal joint common to both parts of the limb.

This remarkable phenomenon was first observed by Weismann [2, p. 167], but it appears to have attracted little or no attention since.

\* I regard the trochanter as part of the femur.

If we compare the thoracic leg of an insect with that of a crayfish, we recognise in the five joints of the insect's tarsus the representatives of the five joints of the crustacean limb known as the basipodite, ischiopodite, meropodite, carpopodite, and propodite, whilst the claw-like dactylopodite is represented in insects by two tarsal claws. In the crustacean the basal coxopodite corresponds with the coxa of the insect, whilst the exopodite of the generalised Crustacea corresponds with the femoro-tibial portion of the limb in the insect.

The bladder-like femoro-tibial rudiment closely resembles

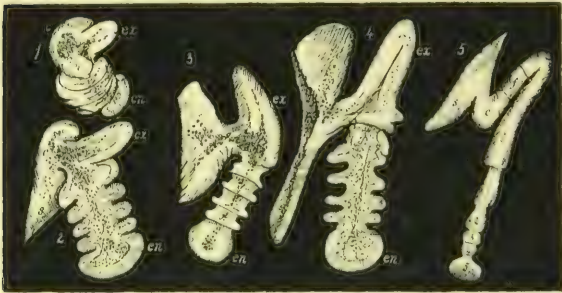


FIG. 34.—Five stages in the development of the leg in the nymph, showing the manner in which the femoro-tibial joints are formed from the exopodite. 1, The rudiment of a limb in the second stage of development. 2, The same in the third stage. 3, 4, and 5, Three successive stages of the same: *c*, coxopodite; *ex*, exopodite; *en*, endopodite; *s*, sternum; *c'*, coxa; *f*, femur; *t*, tibia; 1 to 5, tarsal joints.

the exopodite of some Crustacea, and the rudimentary limb of the fly-nymph takes us back to the primary bifurcate condition still retained in the thoracic limbs of the generalised Crustacea.

This much is certain, the five tarsal joints in the Blow-fly are all differentiated distinctly before any trace of the segmentation of the femoro-tibial portion of the limb is apparent, and this is developed from a process which closely resembles the exopodite of the crustacean limb.

The Dorsal Appendages of the thorax, or wings, are highly

characteristic of the imago in the Insecta, but are confined to the meso- and metathoracic somites.

The wings are sac-like prolongations of the syndesmotic integument between the dorsum and the pleuron; each wing, therefore, exhibits two layers of thin integument one above the other. These are closely united in the mature adult, but in the immature imago or fully-developed nymph they are separated by a layer of spongy cellular tissue, of a reticular character, the spaces of which are blood sinuses continuous with those of the thoracic cavity. In the nymph this tissue is permeated by a brush of dichotomous sub-parallel tracheal capillaries.

The upper and lower layers of integument are termed the upper and lower wing membranes. Diagrammatic representations of the wing-bearing somites are given in most works on elementary comparative anatomy. I shall not, therefore, reproduce them here.

**The Homology of the Wings.**—The wings are developed from the edges, epipleura, of the dorsal plates of the meso- and metathorax.

The edge of the dorsal plate of the prothorax closely resembles the epipleuron of the Crustacea, but never attains the characters of a wing. In the Cockroach larva both the meso- and metathorax have precisely similar edges to the dorsal plates; within these the wings are developed. The rudimentary elytra of the female Cockroach are manifestly a modification of the edge of the tergum of the mesothorax.

In many aquatic larvæ leaf-like appendages occur on both the thoracic and abdominal dorsal plates, in the position of wings. These leaf-like appendages contain tufts of tracheæ, and have the function of gills. Graber says: In the young larvæ of the Termites, which live in damp places, similar tracheal gills occur on the thoracic and abdominal dorsal plates, and the development of the wings is effected by the enlargement and modification of those which belong to the meso- and metathorax [10, Bd. 1, p. 190].

The tracheal gills of insects are, moreover, very similar to

the dorsal gills of the annelids, so far as their position is concerned. It appears probable, therefore, that the wings are a modification of the respiratory organs of some ancestral form.

Although our knowledge of the more generalised *Insecta* goes far to render it certain that the earliest forms of insect life were entirely terrestrial, and that the aquatic habits, like the vermiform condition of the larvæ, are acquired, or intercalated modifications, the conditions observed in the *Termites*, and the existence of temporary tracheal brushes in the rudiments of the wings of the fly-nymph, show that the terrestrial habits of the earliest and most generalised insects cannot be used as arguments against the view first enunciated by Gegenbaur,\* that the wings of insects are modified gills which have entirely lost their respiratory, and have assumed a new function, that of aerial locomotion.

**Development of the Wings.**—The wings first appear as papillæ of the epiblast, which soon exhibits a cavity filled with stellate mesoblast and blood. This sac-like wing becomes broad and flattened, so that it presents an upper and a lower wall, and a tuft of nearly parallel and very numerous tracheal vessels is developed in the wing cavity. The walls of the wing sac become plicated in fan-like folds radiating from its attachment to the thorax. The angles of the folds become thickened, and form the primary nervures.

A chitinous epidermis is deposited on the surface of the wing sac. In many nymphs this attains considerable thickness, and appears externally when the larval integument, under which the wing is formed, is shed.

The first cuticular layer does not persist in the imago, but is shed after a second cuticular layer—the permanent cuticle of the wing which becomes the wing membrane—is deposited. The nervures are developed on the convexities of the primary folds, and in the corresponding grooves of the opposite surface of the wing sac.

The tracheal vessels of the wing remain only in the young

\* 'Grundzüge der Vergl. Anat.'

nymph; they are afterwards absorbed. When the imago emerges from the pupa, or when the cuticle which covers the nymph is shed, the mesoblast and hypoderm of the wing are both present, so that the wing is still a sac communicating with the thoracic cavity and permeated by a rich plexus of blood sinuses. It is small and thick.

After the emergence of the imago the wing rapidly expands in length and breadth, at the same time decreasing in thickness. The upper and lower surfaces are drawn together by the contraction and atrophy of the mesoblast, and subsequently of the hypoderm, except at its junction with the thorax and in the course of the largest nervures; where, the wing cavity persists, and its mesoblast develops small tracheæ, blood sinuses and tendinous cords connected with the smaller wing muscles. The greater number of the nervures become solid chitinous rods, and appear as convex ridges on both surfaces of the wing. Between these the wing membranes come into contact, and all the epiblastic and mesoblastic cells disappear.

**Structure of the Wings.**—The wing membranes are supported and extended by branching hollow or solid nervures, which form a reticulated framework. These are chitinized thickenings of one or both wing membranes. The number of nervures, their manner of branching, and the extent of the reticulation between their branches, vary greatly, but there is a general agreement in the arrangement of the principal nervures at the attachment of the wing with the thorax in all insects.

**In the Dragon-flies** the four wings are alike, and these insects exhibit a very generalised type of wing. In other insects the wings deviate more or less from this type, without, however, altogether departing from it.

The wings of the Dragon-flies exhibit an anterior and a posterior margin, a rounded apex, and a truncated base which corresponds to its thoracic attachment.

The anterior part of the base is folded fanwise, so that it exhibits three ridges and two furrows above, and two ridges below. This portion of the wing is strengthened by five strong nervures, one corresponding to each ridge.

The posterior part of the base remains membranous, and forms an axillary fold which checks the forward movement of the wing. I shall term the dorsal nervures costal, subcostal, and patagial; and those of the ventral ridges hypocostal and median nervures. The costal nervure forms the anterior thick margin of the wing. The wing membrane at its attachment to the thoracic wall dips downwards and backwards between the costal and hypocostal, or second nervure; it then ascends nearly perpendicularly to the subcostal. It descends backwards to the median, and reascends to the patagial nervure.

The three superior nervures terminate on the dorsal aspect of the thorax in three tubercles, which articulate with the edge of the dorsal plate.

The anterior tubercle supports the marginal nervure. The median tubercle is a complex sclerite, very narrow above where it bears the subcostal nervure, but broad below where it supports the hypocostal; the posterior tubercle terminates in the median and patagial nervures.

The wing joint, therefore, consists of three parts; each capable of independent movement, and acted upon by special muscles. I shall term them respectively the pro-, meso-, and metapterygium.

These are present in the wings of every insect I have examined. The pro- and mesopterygium are generally more largely developed in the anterior wing, whilst the metapterygium is more developed in the posterior wing.

**Movements of the Wings.**—The wings move in the horizontal and vertical planes; the forward movement is extension, the backward flexion. The upward and downward movements are elevation and depression.

The wings are further capable of rotation on their own long axis; this action is similar to the feathering of an oar, and is of the utmost importance in the mechanism of flight. I shall term it rotation.

The Wing Joint admits, therefore, of flexion, extension, elevation, depression, and rotation, although the extent

of each varies greatly in different insects. In the generalised Neuroptera and even in *Æschna*, the only movements which are at all extensive are those of elevation and depression; rotation is limited, and flexion and extension are still more limited—hence the wing joint is comparatively simple. Rotation is mainly effected by the simultaneous elevation of the pro- and depression of the metapterygium, or *vice versa*. In the Hymenoptera and Diptera rotation and flexion are provided for by the segmentation of the pterygia, which consist of complex sclerites uniting the rigid nervures with the thoracic wall. These sclerites form a wing root which has some resemblance to the carpus of a vertebrate. The sclerites articulate with each other by complex surfaces, not only in series, formed by the segmentation of the roots of the main nervures; but laterally, those of the propterygium articulating with those of the mesopterygium, and those of the mesopterygium with those of the metapterygium.

In the more highly modified Insecta there is a constant tendency towards the reduction of the wings to a single pair, either by a locking mechanism which unites the posterior border of the anterior with the anterior border of the posterior wing, or by their function as an organ of flight being in abeyance in one or other pair. A few insects in all orders are apterous.

In the Diptera the anterior wings only are organs of flight; the posterior pair are greatly reduced in magnitude, and form complex sensory organs, which are known as halteres, or balancers.

Owing to the almost equal development of both the anterior and posterior wing roots and systems of nervures in the Diptera, the wing often appears to consist of both an anterior and a posterior wing united, its anterior half closely resembling the anterior, and its posterior half the posterior, wing of the Hymenoptera. There can be, however, no question as to their being the homologues of the anterior wings only, nor as to the homology of the posterior wings with the halteres. The only authority who ever questioned this

homology was Latreille, who regarded the halteres as abdominal appendages. I shall show hereafter that Latreille was clearly misled by the attempt to prove that the first abdominal segment enters into the composition of the thorax in the Diptera.

The posterior margin of the wing is usually prolonged, in all the Diptera with a heavy abdomen, in the form of two semicircular scales, the anterior of which is the squamula, or lesser wing scale, and the posterior the squama, or great wing scale. Those Diptera which possess wing scales are termed calypterate.

**Modifications of the Thorax.**—Graber says, in speaking of the thorax in insects generally: 'It is especially an organ of locomotion; in the more terrestrial forms the three thoracic segments are mobile on each other; in aerial insects, on the other hand, they are consolidated and form a rigid case, in which the segment bearing the largest pair of wings is most developed. The sternal region is chiefly developed in relation to the legs, and when the three pairs are equal in size, the three sterna are also more or less equally developed, whilst the pleura and terga are largest in the wing-bearing segments. Whenever the wings are reduced, there is a corresponding reduction of the dorsal arch' [10, vol. 1, p. 85].

In illustration of the above statements, I would observe that in the Coleoptera, in which the mesothoracic wings are reduced to wing covers, or elytra, which serve as mere protective sheaths, the dorsal arch of the mesothorax is much reduced. In the Diptera, on the other hand, it is the metathorax which has a rudimentary dorsum, and the whole segment is greatly reduced. The coleopterous metathorax resembles the dipterous mesothorax, and may be compared with it, almost every sclerite of the one occurring in the other.

In all aerial insects the prothorax is also greatly reduced in size; thus, in the Lepidoptera and Hymenoptera the dorsal arch forms a mere collar (*collare*). It is also separated from the sternal portion by a syndesmosis, a fact which led Kirby and Spence to deny the prothoracic origin of the *collare*.

In the Diptera the dorsal arch of the prothorax forms a narrow rim, which is not visible without dissection.

It would, perhaps, be hazardous to give a more detailed description of the thorax applicable to insects generally, and any attempt to describe the various modifications of the exo-skeleton would be foreign to my purpose. I shall, however, in the special description of the thorax of the Blow-fly, give such comparative details as are necessary to the correct interpretation of the homologies of its several parts.

#### **b. General Description of the Thoracic Skeleton of the Blow-fly.**

The nomenclature I employ is a modification of that proposed by Osten-Sacken [81] for the sutures, and, as far as possible, that of Audouin [38 and 39] for the sclerites of the meso- and metathorax.

**The Thoracic Skeleton** forms a subovoid capsule, with a cervical opening in front, an abdominal opening behind, and three pairs of ventral foramina with which the basal joints of the legs articulate. There are two large spiracles on each side, the anterior and posterior. It presents for examination a dorsal, a lateral, a ventral, an anterior, and a posterior aspect.

**The Dorsal Aspect** (Fig. 35) exhibits two transverse sulci, prescutal and postscutal. The anterior or prescutal sulcus is faint and separates the prescutum ( $\text{3}^*$ ) from the scutum ( $\text{2}$ ); the posterior or postscutal sulcus is deep and well marked, and divides the scutum from the scutellum ( $\text{1}$ ).

**The Prescutum** is very convex from before backwards; its anterior part, which cannot be seen from above, descends vertically to the border of the cervical opening.

**The Scutum** ( $\text{2}$ ) exhibits a lateral projection, the scutal spine (*Mili*) ( $\text{4}$ ), behind the anterior root of the wing ( $\text{5}$ ). In front of the spine is a depression in which the anterior wing root lies, the pre-alar fossa; behind the spine there is a smaller fossa, the post-alar fossa; and externally to this a deep triangular fissure, the supra-tympanic fissure.

\* The numbers and letters refer to all the figures.

The **Scutellum** (1) is a pouch-like projection overhanging the posterior part of the thorax and the base of the abdomen (Plates VII. and VIII.). It is connected with the scutum by a pair of divergent ridges, which arise from its outer anterior angles; these are the scutellar bridges of Loew [77]. Descending from the root of the scutellar bridge, a process of the scutellum forms the upper edge of the posterior alar-apophysis (Plate VII., *b f*). It bounds the outer edge of

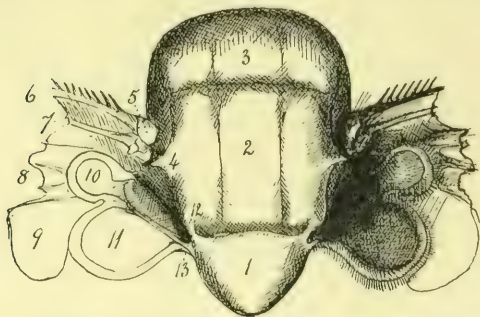


FIG. 35.—Dorsal view of the Thorax of the Blow-fly: 1, Scutellum; 2, scutum; 3, prescutum; 4, scutal spine; 5, propterygium; 6, costal, 7, subcostal and hypocostal nervures forming the remigium; 8, patagium; 9, lobulus of the wing; 10, squamula; 11, squama; 12, scutellar bridge; 13, posterior alar apophysis.

the supra-tympanic fissure, and the great wing scale (11) is attached to it.

The **Lateral Aspect** is represented in Plate VII., Fig. 1. Near its anterior margin the large anterior spiracle (19) will be readily recognised by its orange-yellow colour. Starting from the upper margin of the spiracle, and extending back to the wing root *h*, there is a deep suture, the dorso-pleural suture. It is the anterior part of an extensive syndesmosis (*e, f, g, h*), the alar syndesmosis. Descending vertically from the dorso-pleural suture between the plates numbered 18 and 28 is the mesopleural syndesmosis.

Bounding the mesosternum (30) above and behind is a curved suture, the sterno-pleural; and extending upwards from the sternopleural suture to the posterior spiracle is the hypopleural suture.

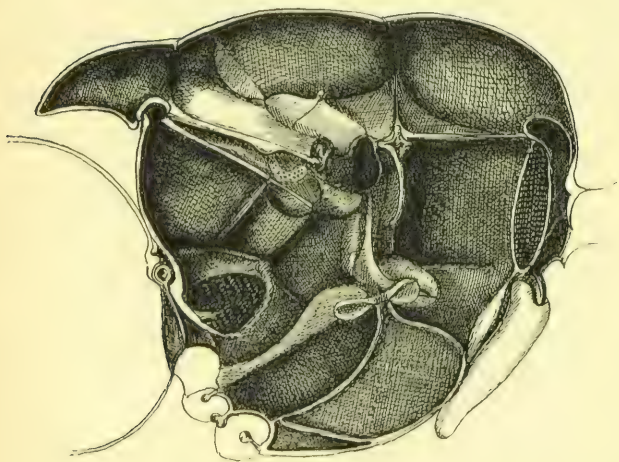
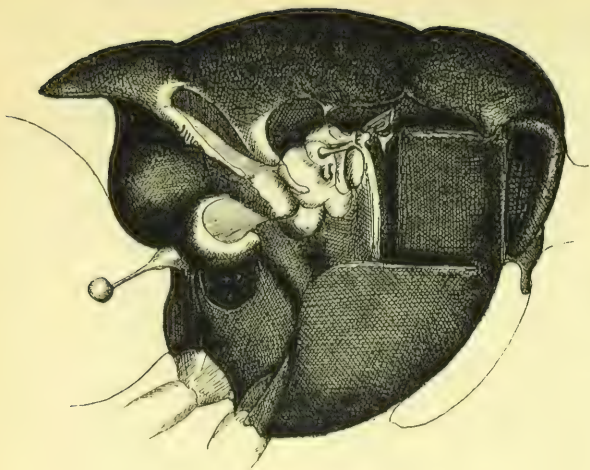
The following plates will be readily distinguished: A large square plate (18) continuous with the mesosternum in front of the sterno-pleural suture. This I term the lateral plate; its nature has been much discussed. I believe it is a portion of the great mesosternum, which in the Bees (*Bombus*) and in many Orthoptera always extends upwards to the dorsum. Brauer incorrectly regards it as the episternum. It is certainly not the episternum of Audouin. In some Lepidoptera and other insects the sterno-pleural suture reaches the spiracle, when the lateral plate becomes a separate sclerite.

The plastron of the mesosternum (30) is the large plate below the sterno-pleural suture. Behind it are the two sclerites of the coxa of the intermediate leg (*p*, *q*) and the lateral part of the metasternum (*43*). Above the latter, the posterior spiracle is situated; and between the hypopleural, sterno-

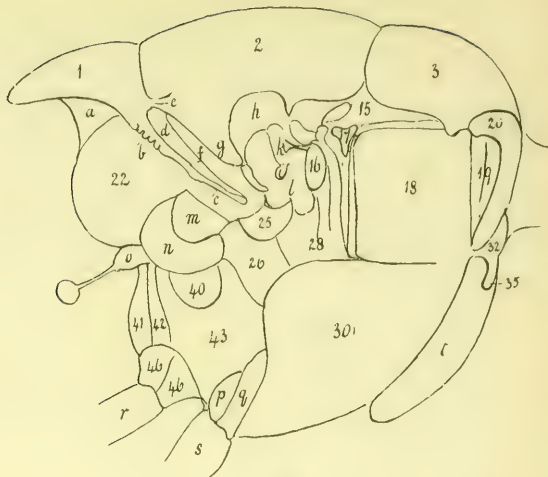
#### DESCRIPTION OF PLATE VII.

FIG. 1, The Exterior, and FIG. 2, The Interior of the Thoracic Skeleton: 1, scutellum; 2, scutum; 3, prescutum; 4, posterior dorso-pleural diarthrosis; 5, great alar apophysis; 6, scutal pouch; 7, ridge on alar apophysis; 8, small tympanic plate; 9, posterior parascutal plate; 10, apodeme of parascuta; 11, anterior parascutum; 12, uncinat process; 13, head of alar apophysis; 14 and 15, anterior alar fossa; 16, great ampulla; 17, parapteron; 18, lateral plate; 19, anterior spiracle; 20, paratrema; 21, tympanic ridge; 22, lateral plate of post scutellum; 23, mirror; 24, tympanic plate; 25, costa; 26, epimeron; 27, ridge between epimeron and episternum; 28, episternum; 29, great entopleuron; 30, mesoplastron; 31, hypotreme; 32, epitrochlea; 33, prodorsum; 34, neck; 35, process of epitrochlea; 36, root of the haltere; 37, ridge above the posterior spiracle; 38, scaphoid process of the mesophragma; 39, the mesophragma; 40, spiracle; 41, epimeron, and 42, episternum of the metathorax; 43, metaplastron; 44, entosternum of metathorax; 45, furca of mesosternum; 46, posterior coxa; 47, intermediate coxa; 48, 49, and 50, articular heads on the meso- and metasterna for articulation with the coxæ; 51, vertical plate of metasternum; 52, mesoplastron; 53, vertical plate of mesosternum; *a*, part of the shield of the postscutellum; *b*, *c*, posterior alar apophysis; *d*, *f*, supra-tympanic fissure; *g*, great alar apophysis; *h*, post-alar fossa; *k*, hypopterygium; *l*, sacculus; *m*, great tympanic membrane; *n*, tympanic bulla; *o*, halter; *p*, posterior, and *q*, anterior sclerites of the intermediate coxæ; *r*, posterior, and *s*, intermediate femora; *t*, anterior coxa.

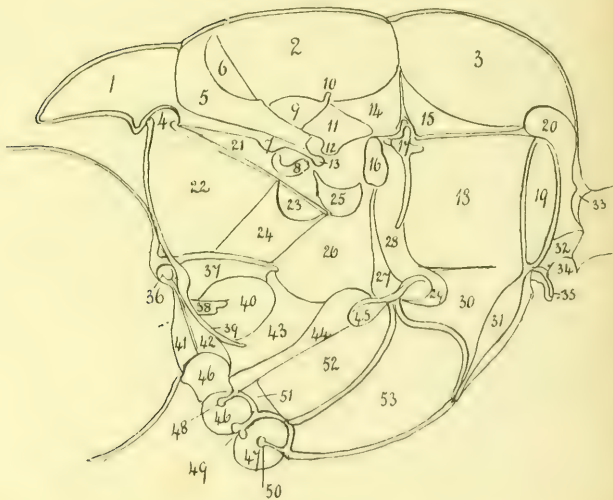


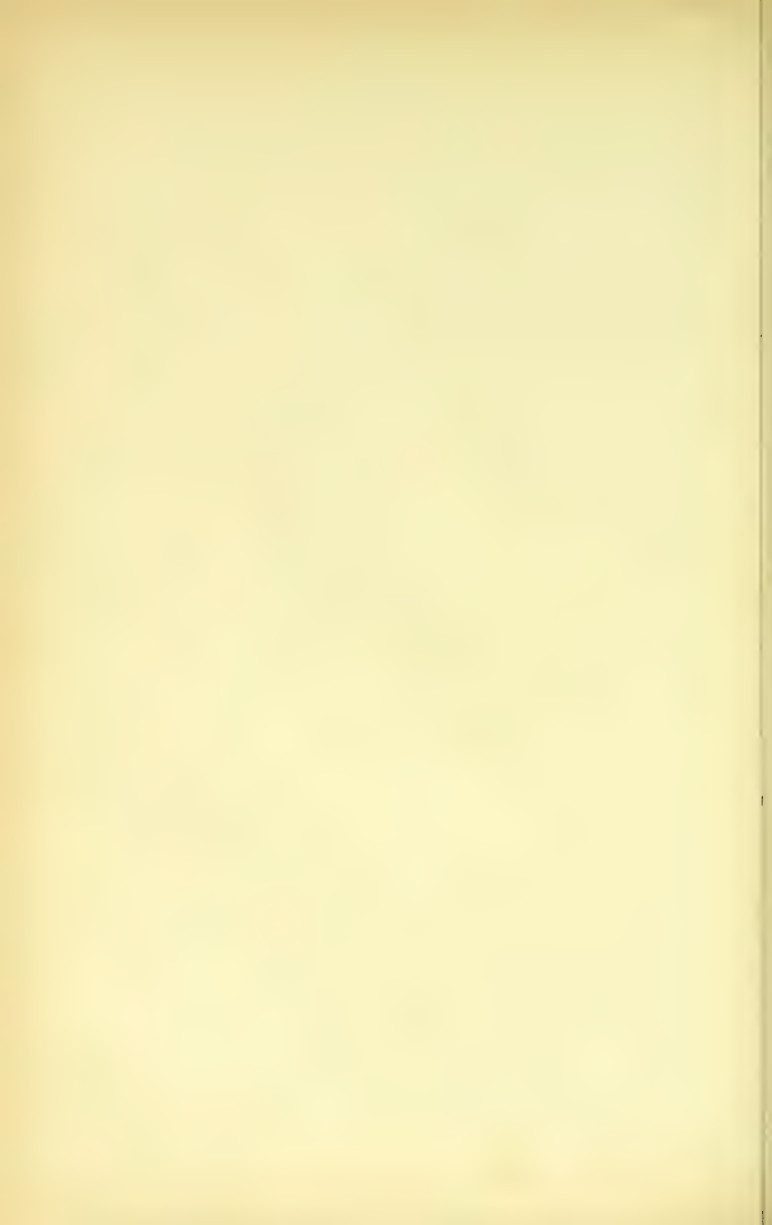


1



2





pleural, and mesopleural sutures and the wing, there is a complex region, the pleuron, consisting of the episternum (28), the epimeron (26), and the costa (25). Behind this region and above the posterior spiracle a convex protuberance is seen. This I term the tympanic bulla (*n*), and between the tympanic bulla and the scutellum there is a large convex plate (22), the lateral plate of the post-scutellum.

All these sclerites, except the metasternum, belong to the mesothorax. Behind the metasternum are the small plates of the metapleuron (41 and 42), with the halter (*o*) above them. These parts are better seen from behind and below.

In front of the anterior spiracle there is a curved plate, which appears in the figure somewhat like a pistol handle. Burmeister [8] called it the scapula, and identified it correctly with the tegula of the Hymenoptera and the scapula of Straus Durckheim. In the Diptera, Fabricius described it as 'punctum callosum ante alam.' It was also called the humerus by the earlier writers. I shall term it the paratrema. It is the representative of the tegula in the Hymenoptera, the operculum of Chabrier. Hammond [78] recognised the fact that this is part of the prothorax. Below it the epitrochlear plate, also part of the prothorax (32), is easily made out.

**The Ventral Surface of the Thorax.**—The greater part of the ventral surface of the thorax looks forwards and downwards. It is formed by the great mesosternal plastron with the prosternal area in front of it and the intermediate coxæ behind it. The posterior part of the ventral surface looks backwards and downwards; it is hidden to a great extent by the intermediate and posterior coxæ.

To complete the examination of the ventral surface the posterior and intermediate coxæ should be removed; the parts exposed will be described in the description of the meso- and metasterna. The suture between the meso- and metasterna I term the transverse ventral suture; it separates the meso- and metathoracic somites, but is not very obvious except on the inner surface of the thoracic wall.

**The Anterior Surface of the Thorax.**—(Plate VIII., Figs. 1

and 2.) To examine the anterior surface of the thorax it is necessary to remove the head. This surface is then seen to be subhemispherical, it consists of the prescutum and paratrema above. Between the anterior thoracic foramen and the prescutum there is a thickened rim, which is separated from the edge of the prescutum by a distinct internal inflection, the prothorax; the ring is undoubtedly the narrow dorsal arch of the prothorax. There are three smooth surfaces above the cervical foramen against which the head rests, an oblong central surface on the prescutum, and a circular surface on each paratrema. Below each paratrema the epitrochlear sclerite (32) overhangs the anterior coxa. This sclerite also articulates with the posterior cervical sclerite, or condyle, which supports the head.

Between the condyles a small saddle-shaped sternum is seen, with two remarkable processes in front covered with long sensory bristles. I shall term it the 'sella' (Plate VIII., Fig. 3).

The under surface of the anterior part of the thorax is closed in by soft, flexible integument. This unites the neck, condyles, prosternum, and anterior coxæ with the mesosternum. I term it the prosternal syndesmotic area, or simply the prosternal area. The integument of this region exhibits several sclerites, which are perfectly distinct and movable on each other in the immature imago, but become more or less completely united with each other and with the mesosternum in the mature insect. The sclerites of the prosternal area will be more conveniently described hereafter; their relations are sufficiently indicated by the figures in Plate VIII.

**The Posterior View of the Thorax.**—To examine the posterior surface of the thorax the abdomen must be carefully removed. The thoraco-abdominal opening is surrounded by the posterior coxæ and a narrow process from the metasternum below, by the metapleura on each side. and above by the post-scutellum.

The post-scutellum consists of a central convex shield and two somewhat triangular convex plates, one on each side, the lateral plates of the post-scutellum.

The posterior angle of the lateral plate of the post-scutellum

forms a convex fold, which supports the abdomen; below the shield of the post-scutellum a large mesophragma projects downwards and forwards into the thoracic cavity, reducing the thoraco-abdominal opening to a crescentic slit. The edges of the mesophragma are connected with the anterior edge of the metapleura, so that it separates the capacious mesothorax from the small metathorax, the cavity of which is thus rendered continuous with that of the abdomen.

The halteres are seen between the upper extremities of the metapleura and the lateral plates of the post-scutellum. Below the halter and in front of it, the great posterior spiracle is very conspicuous, and a convex plate is seen between the upper margin of the spiracle and the lateral plate of the post-scutellum; this is the posterior part of the tympanic bulla.

The scutellum articulates with the upper edge of the shield of the post-scutellum by syndesmosis, and the superior angles of the post-scutellar shield form strong articulations with cavities on each side of the scutellum: this is the posterior thoracic diarthrosis (*Mihi*).

The lateral parts of the metasternum and a portion of the mesosternum are also seen in the posterior view of the thorax, and the great wing scales project above the tympanic bullæ and the lateral plates of the post-scutellum.

### c. The Sclerites of the Thoracic Skeleton.

The **Mesosternum** consists of the mesoplastron, the lateral plates, and the mesothoracic entothorax.

The **Plastron** is formed of two lateral halves, united by a strong inflected suture the entothorax, which appears as a mere line externally. Each lateral half of the plastron is sub-quadrangle and articulates, in front in the middle line, with a quadrilateral plate situated between the anterior coxæ, which I term the manubrium, from which it is separated by the manubrial suture.

On each side of the manubrium the plastron is bounded, in front, by the anterior coxæ and the epitrochlear sclerites, laterally by the lateral plates and the sterno-plural sutures,

and behind by the transverse ventral suture and the intermediate coxæ.

The **Entothorax** (Plates VII., Fig. 2, and VIII., Fig. 4) consists of a subtriangular vertical plate (53), strengthened by cord-like ridges. The apex of this plate supports a saddle-like meso-furca, on which the great thoracic nerve-centre lies.

The vertical plate extends from the manubrial suture to the posterior border of the plastron; it supports a pair of capitate processes behind (50), which articulate with the intermediate coxæ. The horizontal furca is concave above, and supports four spatulate processes, from which muscles moving the legs and wings arise.

The **Great Entopleuron** (29) is the inflected margin of the posterior external angle of the plastron. It is a large oblique plate, which gives origin or insertion to several muscles.

The **Lateral Plate**.—Seen externally, this plate is quadrilateral, and is raised, above and behind, from the surface of the thorax by its deeply inflected margins. In front it is bounded by the

#### DESCRIPTION OF PLATE VIII.

DETAILS OF THE THORACIC SKELETON. FIG. 1, Anterior View of the Thorax: *3a*, smooth surface on the prescutum; *pd*, prodorsum; *s*<sup>1</sup>, sella; *s*<sup>2</sup>, manubrium; *p*<sup>1</sup> and *p*<sup>2</sup>, greater and lesser pectorals; *c*<sup>1</sup>, condyle, with the claviculæ below.

FIG. 2.—The same seen from behind.

FIG. 3.—The Sella and Corniculæ.

FIG. 4.—The Lower Part of the Thorax seen from above: *aa'*, part of the first abdominal ring.

FIG. 5.—The Thorax, with the Abdomen removed, seen from behind: *p d*, post dorsal arch; *t p*, tympanic plate.

FIG. 6.—The Posterior Extremity of the Median Part of the Metasternum.

FIG. 7.—The Pleuron seen from outside: *hp*, hypopterygium; *ha*, hamulus; *epc*, epicosta; *f*, lower extremity of the fissure in the ascending process.

FIG. 8.—The Internal Surface of the Pleuron: *a*, extremity of the tympanic ridge; *sac*, sacculus; *b*, spines forming ridges on the inner surface of the thoracic wall.

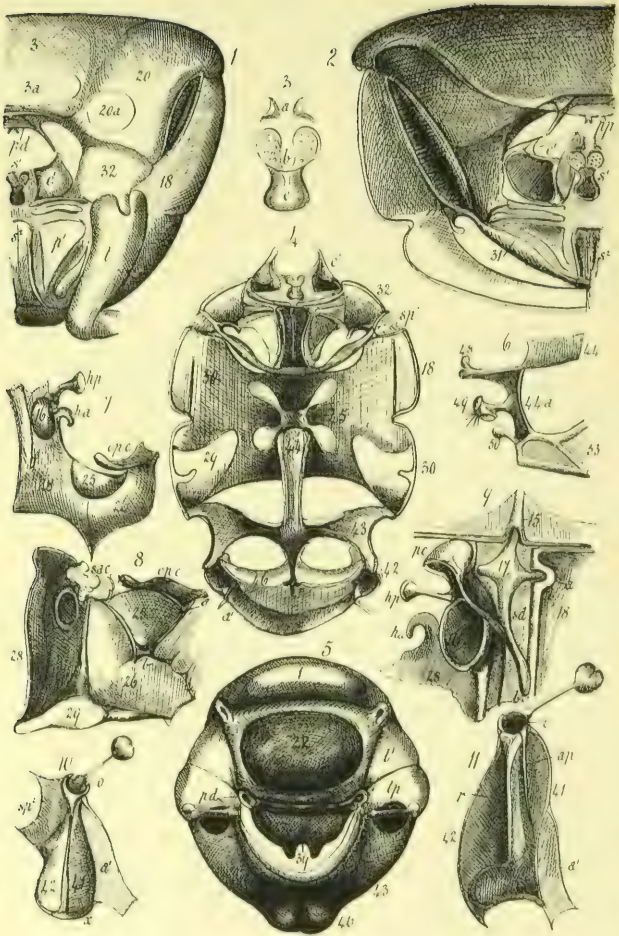
FIG. 9.—The parapteron and its relations, seen from the Interior of the Thorax: *a*, anterior process; *sal*, part of the mesopleural syndesmosis; *l*, long process; *pe*, pre-epaulet; *hp*, hypopterygium; *ha*, hamulus. The wing and sacculus have been removed.

FIG. 10.—External Surface of the Metapleuron.

FIG. 11.—The Internal Surface of the same: *ap*, apodeme of the halter; *a*<sup>1</sup>, part of the first abdominal segment; *r*, ridge between episternum and epimeron; *x*, rail on which the hook of the posterior coxa slides.

The other references to the figures in this plate are the same as in Plate VII.

PLATE VIII.



DETAILS OF THE THORACIC SKELETON.



spiracle and the paratrema; below and in front it is continuous with the plastron, for a short distance; its other relations are sufficiently indicated in the figures. Near the anterior extremity of its superior border there is a small tubercle, which articulates with a corresponding depression in the paratrema; this articulation is the anterior dorso-pleural diarthrosis, it forms the anterior extremity of the dorso-pleural syndesmosis.

Many different views have been held as to the homology of the lateral plate—several of these have been already alluded to. Hammond attempts to identify it with the parapteron of Audouin, but a more careful study of Audouin's writings would have convinced him of his error.

In many insects the corresponding plate is, apparently at least, quite removed from the plastron of the mesosternum by the extension of the pleuron forwards; I believe, however, a narrow neck will be found on careful examination uniting this plate with the plastron.

**The Manubrium** (Plate VIII., Figs. 1 and 2, *s*<sup>2</sup>) probably represents the body of the prosternum. It is a narrow quadrilateral plate, somewhat wider in front than behind; it articulates with the plastron by the manubrial suture. Its inner surface exhibits three sub-parallel ridges—one in the median line, and one on each of its edges; these terminate behind in the manubrial suture. The lateral and anterior edges of the manubrium are continuous with the flexible syndesmotic integument of the prosternal area.

There is a small pouch-like projection on the external surface of the manubrium, close to the manubrial suture, and a corresponding hollow on its internal surface.

The manubrial suture forms an inflection on the inner surface of the ventral thoracic wall, from the extremities of which a pair of strong fusiform processes extend to the lower borders of the anterior spiracles. These processes may be termed the 'hypotremata.'

**The Hypotreme** (Plates VII., Fig. 2, and VIII. Figs. 2 and 4, *3*<sup>1</sup>) extends obliquely across the anterior coxo-sternal foramen, and terminates in three ridges—two ascend and surround the spiracle, and the third curves downwards and forms the external edge of the epitrochlea.

The hypotremata give great strength to the anterior part of the thoracic wall, acting as a kind of stretcher, keeping the external wall of the thorax from being drawn towards the middle line by the action of the muscles which move the head and the anterior legs. As they extend from the suture between the pro- and mesosternum, they may be regarded as the internal continuation of this suture. The spiracle is situated between the pro- and mesothorax, and the suture which forms a ridge in front and behind it is also continuous with the hypotreme.

The epitrochlear sclerite lies in front of the descending process of the hypotreme, and is prothoracic, whilst the lateral plate and the plastron lie behind it, and are both mesothoracic. The hypotreme is a cylindrical rod, between the manubrial suture and the lower margin of the spiracle, and has probably become detached from the posterior margin of the coxosternal foramen by the atrophy of the inflected hypodermis, from which it is developed. I therefore regard the hypotremata the manubrial suture and the spiracles as representing the primary suture between the pro- and mesothorax.

**The Metasternum** is the largest sclerite of the metathorax. It is shaped somewhat like the sphenoid bone of the human skull. It consists of a median longitudinal inflection of the integument supporting a metafurca, of a narrow transverse inflection, and of two lateral plates—the metapleura of Osten-Sacken. These must not be confounded with Audouin's metapleura; I term them 'metaplastra' (Plate VIII., Fig. 4, 43).

The metaplastra are the only parts of the metasternum which are easily seen externally, but when the intermediate and posterior coxæ are carefully separated, a narrow ridge can be distinguished between them: this is the lower edge of the transverse inflected plate; it unites the metaplastra with each other, and is continuous with their anterior and posterior margins.

Each metaplastron is separated from the mesosternum in front by the transverse ventral suture and the intermediate coxa; behind it is in relation with the metapleuron and the first abdominal ring, and externally it surrounds the posterior spiracle.

Seen from its internal surface, the metasternum is cruciform. The transverse vertical plate is the inflection between the intermediate and posterior coxæ; it is joined behind, in the middle line, by a median plate, which is triangular; the upper edge of the latter supports the metafurca, its lower edge articulates with the posterior coxæ. At its junction with the transverse vertical plate it supports a capitellum (49) with which the four coxæ articulate. Its posterior angle bears two divergent capitate processes (48), which articulate with the posterior coxæ.

**The Metafurca** (44) is a long hollow trough from which the

median thoraco-abdominal muscles arise. The posterior extremity of the metafurca is pointed, and dips down between the posterior coxæ; the anterior extremity rests upon the mesofurca.

**The Dorsal Valve.**—If an incision be made through the anterior part of the scutum horizontally backwards until it meets the anterior extremities of the dorso-pleural syndesmosis, the syndesmotic membrane is easily divided, after cutting off the wings close to their roots, as far back as the anterior external angles of the scutellum. Here the dorsum articulates with the post-scutellum by a diarthrosis, the posterior dorso-pleural joint. With a little pains the articulation can be broken through and the remainder of the syndesmotic membrane between the lower surface of the scutellum and the post-scutellum divided. In this way the thorax can be separated into a ventro-pleural and a dorsal valve by the natural articulation, which permits these parts to move upon each other by the action of the powerful sterno-dorsal and longitudinal thoracic muscles. The dissection should be made in an artificial exuvium (see Appendix to chapter).

**The Under Surface of the Dorsal Valve.**—The dorsal valve consists of part of the prescutum, of the scutum, and the scutellum.

The scutum and prescutum when seen from their under surface present an oval fossa, each lateral margin of which exhibits a rim or ridge in front projecting towards the middle line, the dorso-pleural costa, and a strong process behind, the great alar apophysis.

The great alar apophysis (Plate VII., 5) is an inflection of the posterior angle of the scutum, and is separated from the dorso-pleural costa by a deep fissure. It terminates in front in an articular head, which supports the anterior wing-root. Its inner edge is nearly parallel with the inner edge of the dorso-pleural costa.

The scutellum, seen from its under surface, has the form of a conical pouch, the anterior margin of its inferior wall being deeply crescentic, with a thickened rim, the scutellar rim. The anterior extremities of the rim each give off two divergent processes, at the common root of which there is a circular

cup, this cup articulates with a hemispherical process of the post-scutellum, forming the strong posterior dorso-pleural diarthrosis (4). The inferior process of the rim of the scutellum (*b d*) supports the posterior wing-root; this is the alar process of the scutellum. The anterior and superior process (7) extends forwards on the inner edge of the great alar apophysis and forms its articular head (13).

The crescentic rim of the scutellum is united with the post-scutellum by soft syndesmotic integument.

**The Supra-tympanic Fissure** (*f*).—The external surface of the great alar apophysis looks downwards, and forms the anterior part of a triangular inflection of the integument above the great wing-scale. This inflection opens and closes and permits of considerable variation in the capacity of the thoracic cavity; when closed its superior or anterior half rests upon its posterior or inferior half, in which a complex tympanic mechanism lies, and a minute spiracle opens. These will be described in detail in another chapter. The whole arrangement of the supra-tympanic fissure is similar to the infolded gusset of a pair of bellows—the apex of the fold is just in front of the posterior dorso-pleural diarthrosis.

The dorso-pleural costa is the inner edge of the floor of the alar fossæ. It is prolonged forwards as a sutural ridge, which bifurcates and surrounds the paratrema.

The presutural ridge is the inner edge of the presutural sulcus. It joins the two dorso-pleural costæ and supports a cup-shaped cavity in each, which articulates with the head of the parapteron (17). A pair of small plates, which form the inner wall of the posterior alar fossa, articulate with the scutal portion of the dorso-pleural costa. These I term the ‘anterior and posterior parascutum.’

**The Anterior Parascutum** (11) is a distinct oblong plate. Its anterior external angle is prolonged in a curved hook (12)—the uncinatè process—which embraces the anterior head of the dens, a small sclerite on which the propterygium turns when the wing is elevated or depressed.

**The Posterior Parascutum** (9) is inseparably fused with the

edge of the scutum. A small apodeme projects between the parascuta and unites them. It gives insertion to a slender muscle with a long tendon, the action of which is to depress the alar edge of the parascuta and assist in the elevation of the wing.

In removing the dorsum from the thorax, it will have been observed that the prescutum was divided by a horizontal incision just above the anterior spiracle, so that only its posterior part enters into the formation of the dorsum. The prescutum is very convex in front, so that its anterior part forms the anterior wall of the thoracic cavity (Plate VIII., Figs. 1 and 2). The inner surface of this portion of the thorax is best examined by cutting off the anterior part of a skeleton, or artificial exuvium, just behind the anterior spiracle. The prescutum will be seen in such a preparation to be bounded in front by the prophragma and the two paratreemes.

**The Prophragma** (*pp*) is a membranous inflection of the edge of the prescutum. The attached margin of the prophragma corresponds with the junction of the anterior edge of the mesothorax and the posterior margin of the rudimentary prothorax. Its extremities are continuous with the superior and inferior edges of the paratreemes, so that the lateral parts of the prophragma split into two laminæ, like the extremities of the hypotreemes.

The central portion of the prophragma has a free convex posterior border, and exhibits a median projection, strengthened by a distinct bifurcate sclerite. Its upper and lower surfaces are horizontal.

**The Prodorsal Arch** (*pd*) is the inflected edge of the cervical opening of the thorax. It is divided in the median line above into two lateral halves by a distinct suture. Its outer extremities articulate with the anterior margins of the epitrochlear sclerites, and with the inner and lower part of the paratreemes.

Each lateral half is divided into two by a distinct oblique suture, which extends from the attached edge of the prophragma downwards, outwards and backwards, and terminates in a strong apodeme, which projects into the thoracic cavity, the prothoracic apodeme.

**The Paratrema** (20) is seen best from the interior of the thorax. It is a distinct and irregularly quadrate sclerite, bounded above and internally by the prescutum and the prophragma, below by the extremity of the prodorsal arch, and externally by the spiracle, above which it just reaches the lateral plate and the dorso-pleural syndesmosis. Although the limits of the paratrema are not very readily seen externally, they are marked by a very distinct sutural ridge projecting into the thoracic cavity.

**The Epitrochlear Sclerite** is a quadrangular vertical plate, articulating with the paratrema and prodorsum above, and with the condyle by its inner margin.

Its external surface is convex, and projects in a tooth-like process, overhanging the anterior coxa in front.

The external edge of the epitrochlea is formed by the descending process of the hypotreme.

**The Sclerites of the Prosternal Area** are nine in number: the manubrium, two pairs of claviculæ, anterior and posterior, and two pairs of pectoral sclerites, the greater and lesser pectorals.

In the immature imago these sclerites are all distinct chitinous thickenings of the syndesmotomic integument; but in the mature insect the claviculæ are fused with the manubrium and the epitrochlear sclerites.

**The Claviculæ.**—The anterior clavícula is a thin rod of chitin, extending from the anterior edge of the manubrium to the epitrochlea. The posterior clavícula is somewhat shorter and broader, tapering at its extremities.

**The Great Pectoral** is a triangular sclerite, which flanks the manubrium, with its short edge adjacent to the claviculæ.

**The Lesser Pectoral** sclerite is a minute convex caudate fold between the great pectoral and the anterior coxa. It is broadest behind, and is covered with minute bristles.

The claviculæ unite with each other and with the pectorals in the adult insect, and so complete the foramina with which the anterior coxæ articulate.

The integument of the prosternal area is continuous with that of the neck.

**The Neck** is very narrow, sub-cylindrical, and covered by syndesmotomic integument, in which seven sclerites are apparent. These are a median ventral sclerite—the sella, to which allusion has already been made; a pair of accessory pieces in front of the sella—the corniculæ; and two pairs of lateral sclerites: a large posterior pair—the condyles; and a small anterior pair—the epicondyles. There is no dorsal sclerite in the neck of the fly, although two dorsal sclerites exist in the neck of the cockroach [41].

**The Sella** (Plate VIII., Fig. 3) is a saddle-shaped sclerite, with two remarkable transparent lobes in front, which form the lateral and upper walls

of a small median pit in the cervical integument. These lobes are covered with fine sensory bristles, and receive a large number of nerve filaments, which end in special sensory cells connected with the bristles.

This sensory organ resembles similar, but smaller, organs situated on the flexor sides of the limb articulations, and, like these, it is probably concerned in indicating the movements of the parts adjacent to it, by giving rise to sensory impulses originating from movements of the head and fore-limbs, by which the walls of the pit in which it lies are alternately stretched and relaxed.

**The Corniculæ** are two small curved sclerites in front of the sensory lobes of the sella, which form the anterior wall of the pit.

**The Condyles** are subconical sclerosed pouches on the under and outer part of the cervical integument. They exhibit three surfaces: a posterior surface—which rests against the anterior surface of the thorax—an inferior and an external surface. The inferior surface exhibits a curved ridge fringed with hairs, with its convexity inwards. This ridge resembles a rudimentary appendage; indeed, the whole condyle, by a little modification and greater development, might become a chela similar to the post-oral chelæ of Arachnids. The condyle is present in every insect I have examined.

**The Epicondyle** (Fig. 24, *j*<sup>2</sup>) is a rod-shaped sclerite, which easily separates from the condyle in the young imago, but which appears to be inseparably united to it in the adult insect. The epicondyle articulates with the cotyloid cavity of the occipital ring. A small sclerite, the first jugular sclerite of Künckel d'Herculais lies in front of the epicondyle (Fig. 24, *j*<sup>1</sup>).

**Morphology of the Prothoracic Region.**—The discovery of the prophragma has not hitherto been recorded. It undoubtedly marks the posterior limit of the dorsal portion of the prothorax, and confirms the views of Brauer [80] and Hammond [78] as to these limits.

I regard the following sclerites as undoubtedly prothoracic—the prodorsum, paratrems, and epitrochleas, the sella, manubrium, claviculæ and pectorals. The cervical sclerites also probably belong to the prothorax. I have spent much fruitless labour in the endeavour to find some correspondence between these parts and those of the meso- and meta-thorax.

My epitrochlea is certainly the trochantin of Audouin and the rotula of Straus Durckheim. Both the episternum and the epimeron, if they existed, should be behind the epitrochlea, but they are not recognisable. The paratrema appears to me to correspond with the operculum of the Hymenoptera in its double relation with the prodorsum and the spiracle. Hammond assigned it to the prothorax. I cannot accept Brauer's

view that the diaphragma represents the inflected post-scutellum, either in the prothorax or the mesothorax, but think it is indubitable that the prodorsal arch and the paratrems represent the collar of the Hymenoptera.

With regard to the morphological significance of the cervical sclerites, amongst which I have included the sella, they must either be regarded as a portion of the complex prothorax, or as the remains of one or more segments which are no longer distinct in either the embryo or the nymph. I prefer to regard them as prothoracic. Complex prothoracic sterna are frequently seen even in the Orthoptera, for example, in the greatly elongated prothorax of Mantis; and, as I have already observed, the structure of the meso- and metathorax is no guide to that of the prothorax.

The prothorax appears to me to exhibit strong indications in favour of the view held by Patten and others that the thoracic segments have resulted from the fusion of two or more primitive metameres. But any attempt to determine their limits, or even their number, in the absence of direct developmental evidence, could be nothing but guesswork, although it is evident that many metameres have disappeared in the process of evolution.

**The Nomenclature of the Spiracles.** — Whether the anterior spiracle should be regarded as prothoracic or mesothoracic, or the posterior as metathoracic or abdominal, has given rise to much discussion, which I regard as futile, although the views in which it originated are of some interest. Oken's idea of the origin of wings from respiratory organs was adopted by Latreille and De Blainville, and Blanchard appears to have considered them as everted tracheal sacs, the thoracic attachments of which are homologous with the spiracles, and this led him to assert that 'there is never any spiracle on either the meso- or metathorax of a winged insect,' an opinion which has been frequently repeated. Palmen showed that the tracheal gills of *Ephemera* arise independently of the spiracles, and are in no way mere modifications of them, and Blanchard's statements rest solely on the fact that

the larvæ of the Lepidoptera have no spiracles on the segments corresponding with the meso- or metathorax.

Weismann [2] assigns the anterior spiracle to the prothorax on developmental grounds. Hammond [78] adopts the same view. Brauer [80], on the other hand, says it is mesothoracic.

Gosch [79] pointed out the verbal character of the discussion, and his statements may be summarised as follows: It is the rule to describe inter-segmental *abdominal* spiracles as belonging to the segment immediately behind them, and this rule is apparently justified by the fact that when the abdominal spiracles are segmental they are always near the anterior border of the sclerite on which they occur. In the case of inter-segmental *thoracic* spiracles the rule has been reversed, and they have been ascribed to the segment in front of them. Hence the anterior spiracle has been named prothoracic.

It has been asserted that the anterior spiracle in the Coleoptera always remains attached to the prothorax when the latter is separated from the mesothorax. In my experience it as often remains on the mesothorax. I do not, however, think that such evidence is admissible.

Weismann's statements are far more important; the anterior spiracle of the nymph is certainly prothoracic, but it is by no means certain that the anterior spiracle of the imago, which is developed behind that of the nymph, is also prothoracic, as Weismann believed.

It will probably be argued by some that the spiracles are segmental appendages. I regard them as fissures developed in relation with the internal tracheæ, and hold that such fissures may be either segmental or inter-segmental. I have already shown that the anterior spiracle in the Blow-fly lies between the pro- and mesothorax.

The posterior spiracle is between the metasternum and the tympanic bulla, and the bulla is undoubtedly mesothoracic. It is therefore situated between the meso- and metathorax.

**The Pleural Region** is bounded above by the wing roots, in

front by the posterior edge of the lateral plate; below by the sternopleural suture; and behind by the hypopleural suture, the tympanic bulla and the attachment of the great winglet or squama. It is a complex region, which is far larger in the Syrphidæ and Volucella than in the heavy-flying Muscidæ. It contains the following sclerites, which form part of the thoracic wall: The episternum (Plate VII., 28), the epimeron (26), the costa (25), the epicosta (Plate VIII., Fig. 7, *epc*), and the parapteron (Plate VII., 17).

**The Pleuron** (Plate VIII., Fig. 8) is sub-triangular, divided into two by a vertical suture, which projects as a distinct ridge on its inner surface. This ridge is united below with the great entopleuron.

The part in front of the suture is the episternum; that behind it is the epimeron below, and the costa above.

**The Episternum** is an irregular quadrilateral plate, terminating above in two curved processes. These processes are sub parallel; the anterior supports the pre-epaulet of the wing. The posterior process has a hemispherical swelling behind, and below it, the great ampulla (Mihi). The process curves over the great ampulla, and ends in a strong hook, the hamula, which articulates with one of the sclerites of the propterygium. The inner surface of the great ampulla gives origin to a powerful muscle, which acts on the wing root—the ampullar muscle (Mihi).

The episternum is bounded in front by the mesopleural syndesmosis, below by the sternopleural suture, behind by the epimeron, and above by the great ampulla.

**The Epimeron** is much thinner than the episternum; it is irregularly cordate, with the emargination above. Seen from the interior of the thorax, it exhibits a series of radiating ridges, which commence at its margin and form the sutures between the adjacent plates of the thoracic wall; the strongest extends to the external angle of the post-scutellum.

The epimeron articulates—below with the meso- and metasternum, from the latter of which it is separated by the hypopleural suture; behind with the tympanic bulla, and above with the costa.

**The Costa** is a thin shell-like plate. The outer surface is convex, and looks downwards and outwards; it is covered with fine bristles. Its upper edge is continuous with the syndesmosis of the wing, and adjacent to a small sickle-shaped sclerite—the epicosta.

**The Epicosta** presents a strong, chitinated, hollow, curved protuberance in front, which forms a kind of handle to the sickle. I term this projection the 'lesser ampulla'; it gives origin to the lesser ampullar muscle. Künckel d'Herculais [25, p. 98] incorrectly names the epicosta, the 'parapteron,' a term already applied by Audouin to a very different part.

In Volucella and the Syrphidæ the epicosta is prolonged behind as a long cylindrical flexible process, covered by fine setæ. This tail-like process was first described by Chabrier [73, tom. viii., p. 398], who fancifully com-

pared it with the long wing feathers of the birds of paradise. Its use is unknown, but it is probably a sensory appendage.

**The Parapteron** (Audouin), seen from the exterior of the thorax (Plate VII., 17), is a strong heart-shaped nodule, which lies in the mesopleural syndesmosis, just below the dorsopleural suture. It is the head of a powerful lever-like apodeme, which gives insertion to the anterior wing muscles.

**The Post-scutellar Region**, or *Dolium* (Plate VIII., Fig. 5), forms the greater part of the posterior aspect of the thoracic wall. It is bounded above by a syndesmosis, which unites it with the scutellum, and by the posterior alar apophysis, and the insertion of the wing scales; and below by the upper margins of the posterior spiracles and of the thoraco-abdominal opening and mesophragma.

The sclerites which form this region are those of the post-scutellum and the tympanic bullæ. They are united by symphyses, which project internally as strong ridges, and form a kind of sub-hemispherical cap, the *dolium*, which is supported by the lateral plates of the metasternum, with which it is firmly connected by strong internal ridges. It is also articulated with the scutellum by the posterior thoracic diarthroses and by syndesmotomic integument.

**The Post-scutellum** (Plates VII. and VIII., 22) consists of a median shield and two large lateral plates.

The median shield is a very massive sclerite, sub-quadrate in outline, with a concavo-convex centre, convex on its outer surface. Its superior angles are prolonged to form the convex heads of the posterior thoracic diarthroses, and articulate with corresponding concave articular surfaces at the roots of the alar apophyses of the scutellum. Its inferior angles project backwards and upwards into the abdominal cavity and support the first abdominal ring.

The upper edge of this plate is united with the scutellum by syndesmosis, and is strengthened by a thick ridge. Its lateral edges articulate with the lateral plates of the post-scutellum. Its inferior edge has a rim on its posterior surface, the post-dorsal arch, and its edge articulates with the mesophragma. The *os cornutum* of Jurine appears to be the upper edge of the post-scutellum.

The lateral plate of the post-scutellum (Plate VIII., Fig. 5, *l*<sup>1</sup>) is sub-triangular, with the apex of the triangle in relation with the inferior angle of the median shield of the post-scutellum, to which its posterior edge is firmly united; its anterior edge articulates by symphysis with the tympanic bulla; and its superior edge, united with the posterior alar apophysis of the scutellum, forms the inferior margin of the supra-tympanic fissure. This edge is much thickened by a strong internal inflection, which projects into the thoracic cavity; it is continued forwards and downwards into the costal margin of the epimeron (Plate VII., Fig. 2, *22*).

The posterior thoracic diarthrosis is greatly strengthened by the inflected superior and posterior edges of this plate.

**The Tympanic Bulla** (*n*), seen from the side, appears sub-hemispherical, but from behind sub-triangular (Plate VIII., Fig. 5, *tp*): It is the segment of a cone with a convex base. The apex of this cone is in relation with the insertion of the halter. Its upper edge forms a symphysis with the post-scutellum, and its lower edge the upper margin of the posterior spiracle. The lower edge also articulates with the two processes of the metasternum, which form the anterior and posterior margins of the spiracle.

The convex base of the tympanic bulla is deeply notched above and in front, so that a semicircular opening is left between it and a rod of chitin, which extends from the mesopleuron to the upper margin of the tympanic bulla. This is a portion of a strong ridge, the tympanic ridge, between the posterior thoracic diarthrosis and the costal margin of the epimeron (Plate VII., Fig. 2, *21*).

The notch, or foramen, in the bulla is closed by a tense membranous integument (*m*), the membrana tympani major (Mihi), which looks upwards and forwards beneath the great wing scale.

The tympanic bulla, seen from above and in front, resembles a kettledrum, the membrana tympani major being the drum skin. The lowest point of the posterior wing root rests upon the drum membrane. The inner edge of the membrane is attached to the alar apophysis of the scutellum.

The **Mesophragma** (39) is a partial concavo-convex septum, which projects downwards and forwards into the thorax from the lower edge of the shield of the post-scutellum. It is convex behind, and attached above to the post-scutal shield. Its free inferior edge is deeply notched in the middle line, and separated from the lateral walls of the thorax by a narrow fissure on each side, which transmits several small muscles.

The mesophragma has a small, almost square, process, directed forwards and outwards near the upper edge of the posterior spiracle; it arises at the junction of the free and attached margin of the mesophragma.

**Internal Ridges.**—The internal surface of the postero-lateral region of the thorax may be readily examined by making a section in the vertical plane, through the junction of the dorsocentral and lateral parts of the dorsum. This region exhibits two sets of ridges, or inflected sutures—one set radiating from the posterior thoracic diarthrosis, and the other from the inferior angles of the post-scutellar shield.

One ridge is common to the two sets; it is the suture between the shield and the lateral plate of the post-scutellum. Two other ridges radiate from the posterior thoracic diarthrosis. The upper one is the great alar apophysis, the lower the 'tympanic ridge.' The tympanic ridge crosses the tympanic notch, and forms the straight margin of a transparent semicircular plate—the mirror. The convex margin of the mirror is attached to the thoracic wall, dividing the tympanic bulla into two parts (23). Its plane is nearly at right angles to the membrana tympani major, from which it is separated by a narrow space above its free margin. It resembles the mirror of the Cicadæ.

The tympanic ridge extends as far forward as the costal edge of the epimeron.

The ridges from the lower centre are the common one already mentioned, that between the post-scutellum and the tympanic bulla, and the upper margin of the posterior spiracle. The one between the tympanic bulla and the post-scutellum ends in the tympanic ridge, which it joins at a right angle immediately behind the insertion of the great tympanic membrane.

**The Morphology of the Post-scutellar Region.**—The morphology of this region has given rise to very great differences of opinion. Brauer first correctly ascribed it to the mesothorax. Hammond follows Brauer, but incorrectly includes the metasternum in the mesothorax.

Adopting Brauer's view, the posterior spiracle lies between

the meso- and metathorax, and the mesophragma is situated behind the spiracle and immediately in front of the metapleuron. Owing to the great development of the dorsal region of the mesothorax, the dorsal arch of the metathorax is pushed downwards and backwards, and lies on the abdominal surface and lower edge of the post-scutellum, with the halteres between it and the metapleura.

The post-scutellum of the metathorax of the Cockchafer, the tergum of Straus Durckheim, is very similar to the post-scutellum of the mesothorax of the fly; and like the latter, is divided into a central shield, two lateral plates and two tympanic bullæ, although the latter are feebly developed.

The great mobility of the scutellum on the post-scutellar region, and the compact union of the latter with the metasternum, have led some to regard it as a portion of the metathorax; but the relations of the parts amongst themselves, and those of the mesophragma and the halteres show conclusively that the post-scutellar region is mesothoracic.

**The Metathorax** consists of the metasternum, which has been already described, the metapleura and the post-dorsum.

**The Metapleuron** ( $\mu 1$  and  $\mu 2$ ) bears the same relation to the halter that the mesopleuron does to the wing, but, like the appendage which it supports, is reduced to very small dimensions. It is in the form of a nearly vertical isosceles triangle, with its apex upwards.

Its internal surface (Plate VIII, Fig. 11) exhibits three well-marked ridges. The central ridge is nearly vertical; its upper extremity bifurcates and forms a pair of rounded horns, which surround the lower half of the base of the halter. The anterior and posterior ridges are the sutures, in front between the metapleuron and the metasternum, and behind between the posterior edge of the metapleuron and the abdomen.

The metapleuron is therefore divided, like the pleuron, into two parts—the episternum and the epimeron of the metathorax.

**The Episternum** of the metathorax ( $\mu 2$ ) articulates in front with the metasternum, and below with the posterior coxa; above with the post-dorsum and halter, and behind with the epimeron.

**The Epimeron** of the metathorax ( $\mu 1$ ) articulates below with the posterior coxa; behind it is united by syndesmosis with the dorsal arch of the first abdominal segment; above it articulates by its cornu with the halter and post-dorsum; in front it is united by symphysis with the episternum.

**The Post-dorsum** is reduced to the form of a thickened fold, which unites

the cornua of the metapleura ; it lies on the lower edge of the post-scutum, and is connected by syndesmosis with the dorsal arch of the first abdominal segment.

**The Thorax as a whole.**—The numerous complex sclerites of the thoracic wall are united into three groups ; those of each possess little or no movement on each other, and are united by symphysis.

The whole dorsum forms one portion of the thoracic wall, the sterna and pleura a second, and the post-dorsum, or post-scutellum, with the tympanic bullæ, a third.

The sterno-pleural portion of the thorax somewhat resembles an old Spanish ship-of-war. I term it the 'carina.' The post-dorsal portion is firmly attached to the carina and forms a kind of poop, the 'dolum.' The dorsum is attached to the carina by the elastic prescutum in front, and rests upon the four diarthroses. Between the anterior and posterior diarthroses the dorsum and the pleuræ are united by syndesmoses, and a loose syndesmosis connects the scutellum with the dolum behind the posterior diarthroses. The tympanic fissures are oblique extensions of the dorso-pleural syndesmoses, and open and close like the gussets of a bellows. This permits of an increase or diminution of the convexity of the dorsum.

The mesopleural syndesmosis also allows of some variation in the convexity of the carina.

The great muscles which affect the magnitude of the thoracic cavity are the dorsales and sterno-dorsales (Plate XI.).

The contraction of the latter diminishes the convexity of both the dorsum and the carina, closes the tympanic fissure, and increases the breadth of the thorax ; whilst that of the former increases the convexity of the dorsum and carina, closes the mesopleural suture, opens the tympanic fissure, and shortens the longitudinal, but increases the vertical and transverse diameters of the thorax.

Increased convexity of the dorsum and carina renders the dorso-pleural syndesmoses tense, whilst diminished convexity relaxes them. The effect of these movements will be considered hereafter.

The elastic recoil of the thoracic wall acts in antagonism to both sets of muscles, which only counteract each other to a certain degree, both sets increasing the transverse diameter of the cavity.

**The Median Segment of Latreille.**—Before concluding this somewhat lengthy section, I would say a few words on a subject which has been a fertile source of error in relation to the morphology of the sclerites of the thorax in the Diptera.

Latreille discovered that the ventral portion of the first abdominal segment enters into the composition of the thorax in the Hymenoptera. This is especially well seen in those with a sessile abdomen, and anyone who will examine the thorax of a *Cimbex* or *Trichosoma* can easily verify the fact. Latreille calls this segment the 'segment mediaire.'

The median segment of Latreille bears a spiracle, but there is a second spiracle in front of this in *Cimbex*, between the metasternum and the dorsum, corresponding with the posterior spiracle of the Diptera.

This spiracle was unknown to Latreille; it was discovered by Professor Schiödte in 1856 [76].

Latreille erroneously supposed the posterior thoracic spiracle of the fly to be the first abdominal one, and thought that the first abdominal segment enters into the composition of the dipterous thorax. He was, however, more consistent than his followers, for he denied the existence of any homology between the halteres and the second pair of wings. He clearly saw that his theory fell to the ground unless the halteres are regarded as abdominal organs.

At the present day no homology has been more clearly established than that of the halteres and the posterior wings, yet many who smile at Latreille's idea, that they are abdominal appendages, have readily adopted his view of the existence of a median segment in the dipterous thorax. I have shown, I think clearly, that so far from this being the case, the meta-thoracic tergum is abdominal in these insects, the metapleura being on the abdominal side of the mesophragma.

A very complete history of the opinions held on Latreille's 'segment mediaire' is given by Gosch [79].

The remaining sclerites of the thoracic skeleton are those of the legs, wings, and tympanic apparatus, to each of which I shall devote a separate section.

Nomenclature and synonymy of the thoracic skeleton :

- A. **Prothorax**, Audouin. Collare, Chabrier, etc. Manitruncus, Kirby and Spence. Corselet, Straus Durckheim.
  - a. **Prosternum**, Burmeister. Prosternal area, Mihi. Contains the following sclerites :
    - Sella**, Mihi. Cephalo-thorax, Mihi, *olim*.
    - Pectorals**, Mihi.
    - Claviculæ**, Mihi.
    - Manubrium**, Mihi.
  - b. Neck-sclerites, jugulares, are :
    - Condyles**, Mihi. 3<sup>me</sup> jugulaire, Künckel d'Herculais.
    - Epicondyles**, Mihi. 2<sup>me</sup> jugulaire, Künckel d'Herculais.
  - c. **Prodorsum**, or prodorsal arch, Mihi.
  - d. **Epitrochlea**, Mihi.
  - e. **Paratrema**, Mihi. Scapula, Burmeister; *olim*, Humerus.
  - f. Internal parts :
    - Prothorax**, Mihi. Post-scutellum, Audouin.
    - Hypotremata**, Mihi. Belong also to mesothorax.
- B. **Mesothorax**, Audouin. Consists of :
  - a. **Sternum**. Meso-sternum, Audouin.
    - Plastron**, Chabrier.
    - Entothorax**, Audouin.
    - Furca** and median plate, Mihi.
    - Lateral plates**, Mihi.
    - Great Entopleuron**, Mihi.
  - b. Dorsal region :
    - Prescutum**, Audouin.
    - Scutum**, *ibid.*, which bears the
    - Great Alar Apophysis**, Mihi. Processus Styloideus, Chabrier.
    - Scutellum** and **Post-scutellum**, Audouin.
    - Supra-tympanic fissure**, Mihi.
    - Mesophragma**, Brauer. Costa, Chabrier.
    - Lateral Plate of Post-scutellum**, Mihi.
  - c. Lateral region :
    - Pleuron**, Audouin.
    - Parapteron**, Audouin. Clavicle, Künckel d'Herculais.
    - Episternum** and **Epimeron**, Audouin.
    - Costa**, Straus Durckheim.
    - Tympanic Bulla**, Mihi.
    - Dolium**, Mihi. The tympanic bullæ and post-scutellum.

## C. Metathorax, Audouin.

## a. Metasternum.

Transverse and Vertical Plate, Mihi.

Plastron, Chabrier.

Metafurca, Brauer.

## b. Dorsal Arch, Mihi.

## c. Metapleuron, Audouin.

Episternum and Epimeron, Audouin.

## d. Details of the Exo-skeleton of the Legs (Plate IX.).

(For a general description of the ventral appendages of the thorax [legs] see p. 158.)

The three pairs of legs differ chiefly in the form of the coxæ; the remaining joints are very similar in all.

The Coxæ of the anterior legs are tubular and prismatic (Fig. 1, *cx*); those of the intermediate pair, scaphoid, or boat-shaped (Figs. 2 and 3); and of the posterior, pyramidal (Fig. 4).

Each coxa is consolidated and protected by three sclerites; an anterior, a posterior, and an internal plate.

In all the anterior plate is the largest and strongest. It exhibits an internal longitudinal ridge, which terminates

## Bibliography:—

82. POWER, HENRY, 'Experimental Philosophy,' in three books, containing new experiments, microscopical, mercurial, magnetical, 4to. London, 1644.
83. HOOKE, 'Micrographia.' London, 1667.
84. LEEUWENHOEK, A., 'Anatomia rerum cum animatarum tum inanimatarum ope Microscopiorum.' Lugd. Bat., 1687.
85. LEEUWENHOEK, 'Select Works, containing his Microscopical Discoveries,' translated by Samuel Hoole, plates, 4to. London, 1798-1807.
86. DEREHAM, The Rev. W., 'Physico-Theology,' second edition, 1714. An ingenious teleological disquisition, containing a note on the fly's foot, p. 374, and many curious notes on insects.
87. INMAN, THOS., 'On the Feet of Insects.' Proceedings of the Liverpool Literary and Philosophical Soc., No. vi., p. 220. Liverpool, 1849.
88. WEST, TUFFEN, 'The Foot of the Fly; its Structure and Action elucidated by Comparison with the Feet of Other Insects,' Part I., with 3 plates. Trans. Linn. Soc., vol. xxiii. (1859), 1861.
89. LOWNE, B. T., 'On the so-called Suckers of Dytiscus, and the Pulvilli of Insects.' Monthly Micros. Journ., vol. v., 1871.

distally in a peg—the anterior malleolus; this malleolus (*m*) articulates with a depression in the trochanter.

The posterior sclerite always exhibits a thin fenestra (*f*), surrounded by a thick rim; and the latter supports a second peg—the posterior malleolus, which also articulates with the trochanter. When the limb is fully flexed on the coxa, the trochanter lies in the fenestra.

The internal coxal plate is smaller than the others, and completes the inner aspect of the coxal joint.

**The Anterior Coxa** is united by a loose syndesmosis with the sclerites of the prosternal area, and with the margin of the anterior sterno-coxal foramen. Its anterior plate forms a diarthrosis with the projecting process of the epitrochlear sclerite.

The movements of the anterior sterno-coxal articulation are very free: the anterior limbs are not only used as legs, but almost as arms, serving to clean the face and proboscis, and in climbing. These actions depend chiefly on the great mobility of the sterno-coxal articulation, as the prothorax—the *manutruncus* of Kirby—is immovable on the mesothorax. In the predacious Diptera the anterior legs are used in seizing their prey, as in *Empis* and *Dolichopus*.

**The Intermediate Coxa** is lodged in an elliptical depression between the meso- and metasternum (Plate VII., Fig. 1, *p, q*), so that its movements are greatly restricted. The anterior sclerite articulates at its outer extremity by a peg (Fig. 2, *a*) with a deep socket in the mesosternum, on which the coxa rotates about its long axis; this joint permits of a rowing movement of the femur in the horizontal plane in running, and forms what I call a roller-joint. This kind of articulation is very highly developed in some of the geodephagous Coleoptera, as, for example, in *Passalus*.

The wide-open proximal margin of the coxa is connected with the edges of the sternal foramen by a loose syndesmosis, which forms a kind of conjunctiva, in which the coxa moves. The inner plate articulates with the capitellum at the posterior extremity of the mesothoracic entosternum.

The **Posterior Coxa** is articulated with the metasternum, the epimeron of the metathorax, and with the ventral plate of the first abdominal segment. Its movements are more extensive than those of the intermediate coxa, as it is capable of abduction, adduction and rotation. The latter movement is limited by a hook which overhangs a ridge at the inferior margin of the metapleuron, on which it travels as on a rail; this hook springs from the anterior sclerite. The inner sclerite articulates with the capitellum on the entosternum of the metathorax. The freedom of movement in the posterior coxo-sternal articulation permits the posterior legs to be used in cleaning the wings and abdomen.

The **Femur** is a tubular joint; its proximal extremity is partially separated from the rest by deep lateral vertical inflections and forms the trochanter. The constricted part of the femur is strengthened by a ridge-like fold, which is received in a furrow in the trochanter (Fig. 6). This arrangement permits of more or less movement in a horizontal plane, passing through the axis of the femur.

The trochanter is slipper-shaped (Fig. 5). Its proximal

#### DESCRIPTION OF PLATE IX.

- FIG. 1.—The Left Anterior Leg seen from behind.  
 FIG. 2.—The Right Intermediate Coxa seen from behind.  
 FIG. 3.—The Left Intermediate Coxa seen from in front.  
 FIG. 4.—The Left Posterior Coxa seen from behind: *cx*, anterior, and *cx*<sup>1</sup>, posterior, and *cx*<sup>2</sup>, internal coxal plate; *f*, the fenestra; *fe*, femur; *h*, hamulus of posterior coxa; *m*, anterior, and *m*<sup>1</sup>, posterior malleolus; *tr*, trochanter; *sr*, sensory plate; *t*, tibia; *t*<sup>1</sup>, tarsus; *u*, unguis; *p*, pulvillus.  
 FIG. 5.—The Left Anterior Trochanter seen from behind and above.  
 FIG. 6.—The Proximal Extremity of the Left Anterior Femur, with the Trochanter removed.  
 FIG. 7.—The Femoro-Tibial Articulation seen from its inner aspect: *g*, groove in the femur; *cx*, exterior apodeme; *f*, insertion of the flexor muscle.  
 FIG. 8.—The Pulvilli, Claws and Planta of the Anterior Tarsus; ventral aspect.  
 FIG. 9.—Lateral view of the same.  
 FIG. 10.—Upper portion of the Last Tarsal Joint seen from its under surface.  
 FIG. 11.—A portion of the Pulvillus of *Carabus granulatus*, showing the trumpet-shaped setæ, after Tuffen West.  
 FIG. 12.—Tarsal Setæ of *Exoletus hæmorrhoidalis*, after Tuffen West.  
 FIG. 13.—Tarsal Setæ: *a*, of *Mylabris Cichoriæ*, after Tuffen West; *b*, of *Calliphora erythrocephala*, seen with  $\frac{1}{2}$  oil immersion lens.

PLATE IX.



THE LEGS AND FEET.



margin receives the malleolar pegs laterally, and is prolonged internally as an apodeme, which lies within the inner coxal sclerite, and gives attachment to the extensor muscles.

The **Coxo-Trochanteric Articulation** is very complex, and is capable of flexion and extension, also of rotation on the long axis of the femur, and of rotation at right angles to the long axis of the femur on the long axis of the coxa.

The anterior malleolar peg is horizontal, and the posterior vertical. The elevation of the anterior edge of the trochanter throws the tibia forwards, and draws the posterior malleolar peg from its socket; this permits of the depression of the distal end of the femur on the anterior malleolar peg. The elevation of the posterior edge of the trochanter rotates the femur backwards on its long axis, and carries the insect forwards over the tarsus; this movement withdraws the anterior malleolar peg from its socket, and replaces the posterior; the femur is then swung forward on the vertical posterior malleolar peg. In extreme flexion of the femur on the coxa both pegs are in their sockets, and the coxo-trochanteric articulation is locked. Thus in running, when the foot and tibia are thrown back by rotation of the femur, the latter swings forward in the horizontal plane on the posterior malleolar peg; but when the foot is brought to the ground in front of the femoral plane, the distal end of the femur is depressed—that is, the femur is extended on the anterior malleolar peg; a rotation of the femur then urges the insect forwards, and unlocks the anterior and locks the posterior coxo-trochanteric diarthrosis.

The movements of the shank of the femur on the trochanter are apparently very slight, and depend entirely on the elasticity of the integument uniting these parts.

The **Tibia** is sub-cylindrical, slightly curved on its long axis, and thickest at its proximal extremity. It forms a hinge with the femur, the distal extremity of which is hollowed out below for its reception in extreme flexion.

The proximal extremity of the tibia ends in two curved ridges (Fig. 7), which articulate with two grooves in the interior of the lateral portion of the distal extremity of the

femur (*g*). The flexor muscle is inserted into the syndesmosis (*f*) between the femur and tibia on the ventral surface of the limb, and the extensor (*ex*) into the femur dorsally to the articular apodemes. The movements of the femoro-tibial articulation are strictly limited to flexion and extension.

**The Tarsus**, or foot, consists of five joints, each contracted at its proximal extremity, and exhibiting a capitellum, or head, which articulates with a concave socket on the dorsal distal margin of the joint above it. The tarsal articulations are true ball-and-socket joints, which permit of considerable lateral movement, as well as of flexion, extension, and limited rotation. The ventral margins of both the proximal and distal extremities of these joints are united with the adjacent joints by loose syndesmoses. (Fig. 20, *5*, is a diagrammatic representation of this form of joint.)

The plantar surfaces of the tarsal joints support combs of stiff bristles, which are used in cleaning the surface of the integument and the setæ with which it is covered. The comb is most conspicuous on the anterior tarsi, and is rudimentary or absent on those of the intermediate legs.

The terminal tarsal joint supports the pads, pulvilli (*p*), and the claws, ungues (*u*), as well as a plate—the planta or empodium—at its distal extremity.

**The Claws, or Ungues**, are strong, curved, hollow sclerites. Each has a sub-hemispherical head, which articulates with a notch in a thick cordiform swelling on the under surface of the dorsal aspect of the distal margin of the last tarsal joint. The claws of the posterior tarsi are more slender and less curved than those of the four anterior feet.

The upper edges of the claws are united by syndesmosis with the distal extremity of the last tarsal joint.

Some writers regard the plantæ, claws, and pulvilli as a sixth tarsal joint; the rudimentary tarsus of the nymph, however, has only five joints (Fig. 34), so that the claws and pulvilli must be regarded as paired appendages of the last joint. The planta is a sclerite in the extremity of the limb, and not a distinct limb segment.

**The Planta** (Pl. IX., Figs. 8 and 9) is a subquadrate plate, triangular in the posterior tarsus, which articulates with a deep emargination in the plantar edge of the last tarsal joint; it bears a long median setose spine, which projects between the pulvilli. Its inner (upper) surface gives insertion to the strong apodeme of the flexor tarsi muscle, and its lateral edges articulate with the stalks of the pulvilli. These edges exhibit a series of parallel plications or ridges.

**The Pulvillus** is a membranous, somewhat pyriform flattened sac, the narrow neck of which is strengthened by a chitinous ring articulating by syndesmosis with the edge of the planta, and with the distal margin of the last tarsal joint. This ring supports a fan of chitinized ridges, which radiate over the dorsal surface of the pad (Pl. IX., Fig. 10). The pulvilli are the cushions, by means of which flies and some other insects climb windows or walk over the lower surface of glass, or other smooth and polished bodies.

With an oil immersion ( $\frac{1}{12}$ ) the pad is seen to be covered on its under surface with papillæ, arranged in very regular rows, each papilla having a minute orifice at its extremity. Towards the edges of the pad these papillæ become longer, and give place to long, hollow setæ, with trumpet-shaped orifices, which form a dense fringe projecting beyond the edges of the pad.

Henry Power [82] is the first author who mentions these pads, and his description of the feet of the fly is so curious that I shall give it in extenso. He says:

‘She (the fly) hath six legs, but goes only upon four; the two foremost she makes use of instead of hands, with which you may often see her wipe her mouth and nose, and take up anything to eat. The other four legs are cloven, and armed with little clea’s, or tallons (like a Catamount), by which she layes hold on the rugosities and asperities of all bodies she walks over, even to the supportance of herself, though with her back downwards, and perpendicularly invers’d to the Horizon. To which purpose also the wisdom of Nature hath endued her with another singular Artifice, and that is a fuzzy

kinde of substance like little sponges, with which she hath lined the soles of her feet, which substance is always repleated with a whitish, viscous liquor, which she can at pleasure squeeze out, and so sodder and be-glew herself to the plain she walks on, which otherways her gravity would hinder' (p. 5).

This statement of Power's was subsequently controverted by Leeuwenhock [84], who supposed that the minute hairs on the pads have a hold even on the polished surface of glass, and act as tenterhooks; whilst Derham [86] suggested that the pads act as suckers, and that the insect is supported by atmospheric pressure. This view has been the popular one ever since, but Blackwall\* and Inman [87] reverted to Power's original suggestion, which is certainly the correct one.

The minute size of the papillæ and setæ on the under surface of the pads formerly made their investigation exceedingly difficult, but the great similarity of these to the so-called suckers of *Dytiscus*, and the pulvilli of the *Harpalidæ*, has long been recognised. Tuffen West [88] compared the pads of the *Diptera* with the pulvilli of the *Coleoptera*, and gives a large number of beautiful and elaborate figures of the pads of various insects, which are most accurate in all their details. West supposed that the separate setæ act as suckers. In 1871 I showed at the Royal Microscopical Society that the great water-beetle remains suspended by its so-called suckers in a very perfect air-pump vacuum [89]. Flies also walk perfectly well over the exhausted dome of an air-pump. Gilbert White, in his 'Natural History of Selborne,' records some interesting observations which he made on flies in autumn, when they are feeble. He states that they often struggle to remove their feet from glass as if they were firmly glued to its surface. In my former work on the Blow-fly [62], I made the following statements, which still represent my views on this subject:

'There is no essential difference in the pads of flies and the pulvilli of beetles, moths, and other insects; a similar fluid is

\* 'Remarks on the Pulvilli of Insects.' *Trans. Linn. Soc., Lond.*, vol. xvi., p. 767. 1883.

secreted in all. The only difference is that the pads of flies are membranous and transparent, instead of hard and opaque.

'The feet of the smaller house-fly (*Musca corvina*) are the best to show the manner in which the viscid fluid exudes from the extremities of the trumpet-shaped hairs, as they are very large in this species, and a glistening bead of fluid can be seen plainly at the extremity of each hair by placing the living insect under the microscope. The footprints left upon glass by flies consist of rows of dots corresponding to these hairs; this is best seen in those of the lesser house-fly from their greater size.

'The whole appears precisely analogous to the manner in which caterpillars and spiders suspend themselves by silken threads. In both cases the fluid is exuded from minute pores, and bears the weight of the insect, the only difference being in the nature and quantity of the fluid exuded. Much discussion has arisen as to the manner in which flies liberate their feet, and it has even been objected that they would become so firmly adherent after a time that the insect would be glued to the spot. Nothing can be more simple than the arrangement by which the foot is liberated, and in the healthy insect the secretion probably never becomes solid as long as it remains in contact with the foot. It is sufficiently glutinous, even in the fluid, or rather semi-fluid, state it assumes as it exudes, to sustain the weight of the insect, when the strain is put equally upon all the hairs, of which there are about 1,200 on each pad; but when the pad is removed obliquely, so that each row is detached separately, the resistance amounts practically to nothing.

'The direction and length of the hairs upon the pad are so adapted to the oblique direction in which the strain is put upon them when the tarsus is straight, that the insect has a perfectly secure hold; this is immediately released as soon as the tarsus is curved, which is effected by the long slender tendon of the flexor tarsi. In the small house-fly the pads themselves are capable of being curved, for the tarsal tendon branches, and is inserted into the distal extremity of each pad.'

The adhesive fluid which covers the plantar surface of the pads is secreted by a pair of simple saccular glands. These occupy the greater part of the cavity of the four last tarsal joints. The secretion exudes through the hollow papillæ and hairs, often so rapidly when a fly is captured and held between the finger and thumb by the thorax, that it forms small glistening drops on the pads, and may be collected on a slip of glass, when it immediately becomes solid. The tarsal secretion solidifies equally well under water, in which the coagulum is quite insoluble.

#### e. The Wings and Mechanism of Flight. (*Plate X.*)

It is well known that the wings of insects generally present three well-marked areas or regions—the costal, median, and posterior or anal areas.

These areas are easily distinguished in the wings of the *Diptera*; the costal area is bounded behind by the great subcostal nervure, and in front by the margin of the wing. The median area is also called the disc or discal area, a term which I prefer to median. The disc is bounded behind by the median nervure. The posterior area I shall term the ‘patagium’; it is folded when the wing is flexed, and is supported by the

#### **Bibliography:—**

90. BORELLUS, J. A., ‘*De motu animalium*,’ 4to, 2 vols. Lugd. Bat., 1710.
91. PETTIGREW, J. BELL, ‘On the Mechanical Appliances by which Flight is attained in the Animal Kingdom.’ Linn. Soc. Trans., Lond. (1867), 1868, vol. xxvi.
92. MAREY, E. J., ‘*Animal Mechanism: a Treatise on Terrestrial and Aërial Locomotion*,’ 1873; 2nd edit., 1874. Internat. Sci. Ser., vol. xi., Paris and London.
93. LENDENFELD, R. VON, ‘*Der Flug der Libellen; ein Beitrag zur Anatomie und Physiologie der Flugorgane der Insecten*.’ 7 plates and figures. Sitzungb. der K. Akad. Math. Naturwissen. Cl., Wien. Bd. lxxxiii., pp. 289-376, 1881.
94. ADOLPH, E., ‘*Die Dipterenflügel, ihr Schema und ihre Ableitung*.’ Nov. Act. C.L.C. Acad., Bd. xlvii., 1885.  
This paper is entirely systematic.
95. AMANS, P. C., ‘*Comparaisons des Organes du Vol dans le Serie Animal*.’ Ann. Sc. Nat. Zool., ser. vi., tom. xix., 1885.

This paper is of great length, but is inaccurate and does not advance our knowledge of the subject.

metapterygium, from which all its nervures arise. Behind the patagium in the Blow-flies a small segment is separated from the rest of the wing by a notch (I term this the 'lobulus'), and behind the lobulus are the squamula and the squama.

The nomenclature of the nervures which I have adopted will be sufficiently understood by the figure (Pl. X.).

**The Wing-Roots.**—The wing of the Blow-fly is apparently supported by only two roots; an anterior, from which the nervures of the marginal and discal areas arise, and a posterior, which supports the nervures of the patagium.

The anterior wing-root consists, however, of the united pro- and mesopterygium. It presents five carpoid sclerites; these support the marginal and the common root of the subcostal and discal nervures, which I term the 'remigium.' Its movements are quite independent of those effected by the metapterygium.

The carpoid sclerites are arranged in a proximal and a distal series. I term the proximal sclerites the epaulet and the dens; they articulate with the dorsum and with the sclerites of the distal row. The latter are the sub-epaulet, the coracoid, and the unguiculus (Mihi); they articulate with the pleuron, with the proximal sclerites, and with the marginal nervure and the remigium.

**The Dens** (Pl. X., Figs. 7-9) consists of a body and three processes. The body is irregular in form, narrowed in front, forming the neck, which supports an oval convex scale, seen between the epaulet and the coracoid. The neck terminates in a rounded head concealed by the scale, this articulates with a socket formed by the uncinate process of the anterior parascutal plate. Behind, the dentate process projects downwards and backwards, and lies upon the posterior surface of the unguiculus. Internally, there are two processes, an anterior, which projects inwards and forwards and receives the insertion of the accessory elevator muscle of the wing. The second or posterior process is far larger; its distal extremity articulates by a cup-shaped cavity with the head of the great alar apophysis; a line joining the head of the dens with this cup-shaped cavity may be termed the axis of the dens—it is the axis on which the wing is raised and depressed. The direction of this axis undergoes rotation about the head of the dens with increased convexity or flattening of the dorsal valve. Increasing convexity of the dorsum produces the descent of the wing, pushes the alar apophysis forwards beneath the head of the dens, and renders its axis nearly vertical, so that the

anterior margin of the wing descends in a semicircular arc, with its convexity behind and its upper limb vertical. During the ascent of the wing the alar apophysis is drawn back, and the axis of the dens is directed backwards and slightly upwards, hence the anterior margin of the wing ascends in a curve, the upper half of which is convex in front.

When the wing is at rest and flexed, the axis of the dens is nearly horizontal, and the dentate process depresses the patagium and assists in folding the wing.

The Dens occupies the posterior superior part of the propterygium, and only a small portion of it can be seen externally, the dentate process with the neck and the scale.

It is apparently represented in the Hymenoptera by two distinct sclerites, the omoplate and sigmoidea of Chabrier [72, vol. viii., p. 73].

**The Epaulet** (Pl. X., *e*) is a large scale fringed by black bristles, which articulates with the dens behind and with the parascutal plate and the coracoid by syndesmosis; it covers the sub-epaulet, but does not appear to take any part in the formation of the wing-joint, only protecting it in front and above. It does not correspond with the tegula of the Hymenoptera, with which it has been confounded, as this is in front of, and not behind, the anterior spiracle.

#### DESCRIPTION OF PLATE X.

FIG. 1.—The left wing of the Blow-fly.

FIG. 2.—The roots of the same more highly magnified.

FIG. 3.—The base of the marginal nervure and of the Remigium of the left wing.

FIG. 4.—The base of the left Remigium seen from in front and below.

FIG. 5.—The dorsal aspect of the base of the right Remigium.

FIG. 6.—The Epaulets of the right wing, upper and anterior surface.

FIG. 7.—The left Dens seen from above and in front.

FIG. 8.—The left Alar Apophysis and Dens seen from the under surface.

FIG. 9.—The left Dens seen from the interior of the thorax.

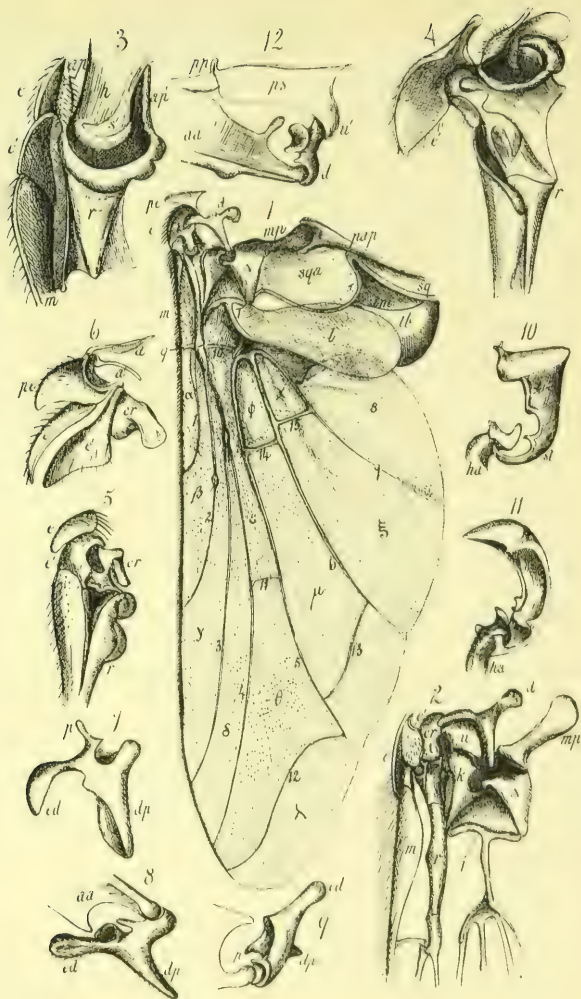
FIG. 10.—The left Unguiculus seen from behind.

FIG. 11.—The right Unguiculus seen from in front.

FIG. 12.—The left Parascuta, Dens and Alar Apophysis.

The following references are the same in all the figures in which they occur: *a*, *a'*, apodemes of the pre-epaulet; *aa*, alar apophysis; *ap*, anterior apodeme, and *ap'*, posterior apodeme of the remigium; *cr*, coracoid; *d*, dens; *dp*, dentate process of the dens; *e*, epaulet; *e'*, sub-epaulet; *ed*, epaulet or scale of the dens; *h*, hypopterygium; *ha*, hamulus; *k*, conoid; *l*, lobulus; *m*, marginal nervure; *mp*, metapterygium; *pap*, posterior alar apophysis (alar apophysis of the scutellum); *pp*, posterior, and *ps*, anterior parascuta; *r*, remigium; *s*, squama; *s'*, hypopterygial sclerite; *sga*, squamula; *st*, stirrup of the unguiculus; *tb*, part of the tympanic bulla; *tm*, tympanic membrane; *u*, unguiculus; *u'*, uncinat process of the anterior parascutum;  $\Delta$ , the deltoid;  $T$ , the tau. Nervures of the wing: *m*, marginal; *1*, mediastinal; *2*, sub-costal; *3*, radial; *4*, ulnar; *5*, median; *6*, sub-median; *7*, anal; *8*, axillary; *9*, anterior transverse; *10*, patagio-hypocostal; *11*, median transverse; *12*, medio-marginal; *13*, discal transverse; *14*, postical transverse; *15*, anal transverse. Areas of the wing: *\alpha*, mediastinal;  $\beta$ , sub-costal;  $\gamma$ , marginal;  $\delta$ , cubital;  $\epsilon$ , prepatagial;  $\theta$ , sub-apical;  $\lambda$ , apical;  $\mu$ , discal;  $\xi$ , patagial;  $\phi$ , anterior basal, and  $\chi$ , posterior basal areas.

PLATE X.



THE WINGS.



**The Sub-Epaulet** (Pl. X., *c'*) is the most anterior of the distal sclerites of the propterygium. It consists of a scale, usually concealed by the epaulet and of a projecting process directed downwards, outwards and backwards. This process is connected with the coracoid by a slender rim of chitin, which apparently acts as a spring, pressing the anterior margin of the wing downwards when fully extended.

**The Coracoid** (Pl. X., *cr*) was described by Chabrier as the beak of the humerus (*bec de l'humérus*), a term applied by him to the base of the nervures of the disc, my remigium. It somewhat resembles the coracoid process of the human scapula, and it prevents the dislocation of the remigium upwards. The coracoid is a perfectly distinct sclerite, wedged in between the epaulet and the unguiculus.

**The Unguiculus** (Pl. X., Figs. 10 and 11) is a complex and important sclerite, which, like the dens, is intimately concerned in the mechanism of flight. It is the 'ongulaire' of Chabrier [72, vol. viii., p. 73]; he confounds it with the remigium, and terms it the base of the humerus in his description of the wing of the cockchafer (*Melolontha*). Jurine termed it 'petit cubitale.'

In the Blow-fly it consists of a horizontal plate, a vertical plate, and a foot.

The superior or horizontal plate is seen from above; it is wedged in between the coracoid and the processus dentatus of the dens. It is sub-quadrate, and has a small claw-like process at its anterior distal angle. This process led me to term it the 'unguiculus.'

The vertical plate descends behind the propterygium in front of the dentate process of the dens; it curves forwards and terminates in the stirrup.

The stirrup of the unguiculus projects below the wing, and forms a hook, which articulates with the hamulus of the episternum (Pl. VIII., Figs. 7 and 9, *ha*); its inferior surface rests upon the sacculus (*sac*).

The anterior surface of the vertical plate forms a socket, in which the head of the remigium rotates. In function it may be compared to the lesser sigmoid notch of the ulna, the head of the remigium representing the head of the radius. The hamulus of the pleuron draws the wing downwards and forwards when the wing is extended; when the wing is flexed (*i.e.*, its anterior margin drawn back in the horizontal plane), the hamulus releases the unguiculus, so that the wing can be freely elevated. The sacculus forms an elastic cushion, on which the foot of the unguiculus rests when the wing is depressed.

**The Costal or Marginal Nervure** articulates with the sub-epaulet, and this articulation permits of a certain amount of elevation and depression. In extension of the wing, the sub-epaulet is rotated forwards under the epaulet by the agency of the parapteron.

**The Remigium** (Pl. X., Figs. 3-5) is the 'tige basilaire de l'humérus' of Chabrier. It represents the united roots of the subcostal and hypocostal nervures, and consists of two parts, an upper and a lower.

The upper part is sub-cylindrical, convex above and concave below; its proximal end articulates by syndesmosis with the coracoid. The lower part is conical, or peg-like, tapering towards its distal end. Its proximal end is hollowed into a deep cup, which is surrounded by a thick chitinated ring (*r*). This ring is free below, but its upper half lies in the lower wing

membrane, which forms two folds, one in front and the other behind the cup. The anterior fold contains a spindle-shaped process (*ap*) covered by numerous sensory hairs. The proximal extremity of this process is connected by an elastic ligament with a strong apodeme, terminating in the upper margin of the pre-epaulet. The posterior fold contains a shorter tooth-like process, into which the tendon of a strong muscle (*ap'*) is inserted; this muscle arises from the upper part of the great ampulla.

When the wing is extended, the cup of the remigium is brought into relation with the hypopterygium, and forms a ball-and-socket joint, on which the remigium rotates.

The **Hypopterygium** is an erectile papilla, strengthened by a curved capitate sclerite, the hypopterygial sclerite, on its lower border and at its extremity. The sclerite articulates with the posterior edge of the pre-epaulet, close to the upper part of the great ampulla. The head of the hypopterygium is covered by a transparent layer of chitin, which has the appearance of an elastic pad. The whole organ is freely movable, and has several small muscles inserted into its base. The movements of the hypopterygium may be observed when the insect is held by the wings; it vibrates rapidly, like the wing, and when the latter is extended it forms a *point d'appui*, on which the remigium moves, and its capitate extremity is brought into relation with the articular cavity in the head of the remigium. In this position it forms a continuation of the remigium, uniting it with the strong ascending process of the episternum.

**Relations of the Episternum to the Anterior Wing-Root** (Pl. VIII., Fig. 7).—The episternum extends towards the dorsum in front of and below the wing—I term this the 'ascending process' of the episternum. The ascending process is divided into two parts by a fissure in front of the great ampulla (*f*). The anterior portion of the ascending process is twisted on its long axis, when the wing is extended, so that its surfaces, which look inwards and outwards below, look backwards and forwards above. Its upper edge supports a hood-like pouch, the pre-epaulet, the margin of which bears the epaulet and sub-epaulet. When the wing is flexed, the anterior part of the ascending process is flat, and it is the partial rotation of its upper end which extends the wing. This is effected by the closure of the mesopleural syndesmosis and the rotation of the parapteron on a vertical axis, so that the outer surface of this sclerite looks backwards and its inner surface forwards. The extension of the wing depends on the contraction of the great longitudinal thoracic muscles, and is the result of the shortening of the thoracic cavity from before backwards. The posterior part of the ascending process bears the great ampulla and the hook or hamulus. The increased convexity of the dorsum also causes the hamulus to descend and draw the wing down by pressing on the stirrup of the unguiculus.

The **sacculus** (*sac*) is a membranous sac which lies beneath the hamulus. It is distended with air during flight so that it supports the foot of the unguiculus, and keeps it in relation with the hamulus. Diminished convexity of the dorsum, with flexion of the wing, releases the hamulus from the foot of the unguiculus, and allows the wing to ascend by swinging on the axis of the dens.

**The Parapteron**, seen from within (Pl. VIII., Fig. 9, 17), exhibits four processes: an ascending process or pivot, which rests in a socket in the dorso-pleural costa, on which the sclerite turns; an anterior process (*a*), which rests against the lateral plate; and an inferior or long process (*b*), which joins the apodeme of the pre-epaulet. The closure of the meso-pleural syndesmosis causes the short anterior process to turn outwards; this movement carries the pre-epaulet forwards in a semicircle, throwing the anterior margin of the wing forwards. A fourth process, behind the body of the sclerite, gives insertion to a muscle which opens the meso-pleural syndesmosis and so drives the anterior margin of the wing backwards, flexing the wing.

**The Metapterygium** (Pl. X, *mp*) consists of a single sclerite, composed of two limbs united at an obtuse angle. The posterior limb or shaft articulates by a sub-cylindrical head with the crutch-shaped extremity of the posterior alar apophysis. The shaft somewhat resembles a humerus, and Jurine called it after this bone; the anterior limb is deltoid in form—I term it the ‘deltoid.’

The shaft of the metapterygium is concave on its under and convex on its upper surface; its outer edge supports the squamula; several muscles are inserted into its concave surface. A strong apodeme projects below its head into the thoracic cavity.

The deltoid articulates with a T-shaped nervure, the tau (*Mibi*), which supports the patagial nervures. The proximal edge of the deltoid presents an anterior and a posterior angle; the former is united with the extremity of the shaft the latter articulates with a conoid sclerite, the conus (*k*), which forms a kind of locking plate between the pro- and metapterygium.

The shaft of the metapterygium is capable of flexion and extension on the posterior alar apophysis, and of rotation on its own axis, as well as of abduction and adduction to a limited extent.

A compound movement, which throws the apex of the deltoid backwards and upwards, raises and opens the patagium; the reverse movement closes and lowers it. Abduction extends and adduction closes the patagial portion of the wing. A simultaneous abduction of the metapterygium and extension of the propterygium extends the wing disc.

An ascent of the anterior angle of the deltoid accompanies an upward movement of the metapterygium, and causes the anterior margin of the wing to descend, by its action on the conus being transmitted to the remigium. This gives the wing a screw surface, with the anterior margin of the wing depressed and its posterior margin raised. The descent of the apex of the deltoid produces an opposite rotation of the remigium, so that the anterior margin of the wing rises and its posterior margin is depressed.

**The Movements of the Wing in Flight.**—If a fly is held by its legs, the wings are frequently seen to vibrate as in flight. The movements of each wing, when seen obliquely from below, produce the optical appearance of a double cone (Fig. 36). The line *abcdefgh* is the locus of successive positions of

the wing apex; *o* represents the thoracic attachment of the remigium and the radiating lines represent the successive positions of the anterior margin of the wing, seen in perspective.

Starting from the point *h* on the curve, the wing plane is approximately vertical, the dorsal surfaces of the two wings turned towards each other, and the apex of the wing in front of the wing-root. In passing from *h* to *a*, the anterior borders of the two wings are nearer each other than the posterior borders, so that the insect is driven forwards by the backward movement of the wings.

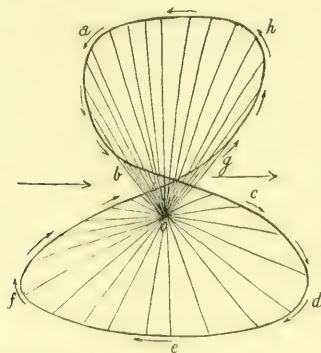


FIG. 36.—A Curve showing the loci of a point at the tip of the wing during flight, seen from below the horizontal plane passing through the wing-roots.

During the descent of the wing from *a* to *b*, the plane of the wing is at right angles to its movement, so that the insect is borne upwards, and at *b* the wings lie in the horizontal plane. From *b* to *c* the wing slopes so that its plane corresponds with the plane of movement, the front edge of the wing cutting the air.

The movement of the wing in the plane *ob od* is due to the combined swing of the propterygium on the axis of the dens, and the extension of the propterygium.

When the wing-tip arrives at the point *d*, the metapterygium is raised, and the deltoid, acting through the conus, causes a rotation of the anterior part of the wing on the remigium. From *d* to *f* the wing sweeps backwards, and the wing plane is inclined to the plane in which it moves at an angle of about  $45^\circ$ , its dorsal surface looking upwards and forwards. The anterior part of this lower back-stroke is the most powerful agent in propelling the insect forwards; but owing to the inclination of the wing plane, it also assists in the upward movement. The lower back-stroke is due to flexion of the wing; towards the end of it the sterno-dorsal muscles contract, the meso-pleural fissure opens, and the foot of the uncinat sclerite is released from the hamulus. The up-stroke, *f* to *h*, is effected by the combined extension of the wing and an upward movement on the axis of the dens; during the upper back-stroke the hamulus is again brought into relation with the foot of the uncinat sclerite, and when the apex of the wing arrives at the point *a* of the curve, its descent is brought about by the contraction of the great longitudinal thoracic muscles, which increases the convexity of the dorsum, causes the hamulus to descend, and extends the wing by closing the meso-pleural syndesmosis.

It will be observed that the wing plane makes three rotations on the remigium. The first at the end of the descent of the wing, by which its anterior margin is depressed. The second rotation occurs when the hamulus escapes from the uncinat sclerite at the end of the lower back-stroke; the anterior margin of the wing is raised, so that the wing plane and the plane of motion upwards correspond. The third rotation is effected at the end of the upper back-stroke; it brings the hamulus into the stirrup of the uncinat. It occurs when the wings stand upwards over the back, and renders the planes of the two wings parallel.

During the two back-strokes the insect is urged forwards; during the first half of the descending stroke it is raised, and the sudden rotation of the wing at the commencement of the lower back-stroke has a similar effect. The forward

movement of the wing both in its descent and its ascent occurs when the wing plane and the plane of movement correspond; hence neither materially affects the onward or upward movement of the insect. The precise manner in which the varied movements of the wing are brought about will be understood by a study of the articulations of the pterygia. The movements of the wings are capable of almost infinite variations, by which the direction and velocity of flight are regulated.

Much has been written on the mechanism of flight in insects. Jurine [72] first discovered that the wings are moved in the Hymenoptera by an alteration in the form of the thoracic wall, the depression of the dorsum raising, and its increased convexity depressing the wing; movements which he correctly attributed to the action of the dorsal and sterno-dorsal muscles. Chabrier [73] figured and described the wing-joints and the parts of the thorax concerned in flight, but except from an anatomical point of view added little to Jurine's exposition. Pettigrew [91] seems to have been the first to discover the curve made by the wing apex and the forward direction of the descending stroke; he also lays much stress on the rotation or screw movement of the wings; he says: 'All wings obtain their leverage by presenting oblique surfaces to the air, the degree of obliquity gradually increasing from behind forwards and downwards during extension, when the sudden or effective stroke is being given. To confer on the wing the multiplicity of movement which it requires, it is supplied with a double hinge or compound joint, which enables it to move not only in an upward, downward, forward, and backward direction, but also at various intermediate degrees of obliquity.' Marey [92] demonstrated the figure-of-eight or loop described by the wing.

No one, except Lendenfeld [93], to whose work I shall presently refer, has preceded me in the attempt to define the exact movements of, and the part played by, the several sclerites of the wing-roots.

Marey [92] believed that the rotation of the wing results

from the action of the air on its surfaces, and made a model of a wing with a stiff anterior border, which he states rotates like the wing of an insect. It may be remarked that a screw movement which results from the resistance of the air would not assist in the support of the insect or in its forward movement, although it might resemble the movements of flight; the screw of a steamer merely turned by a current of water does not urge the steamer on, yet its movement resembles that produced by the engine which drives the vessel.

Marey, moreover, knew nothing of the structure of the wing-joint. He says: 'The exceedingly complicated movements of the wing would induce us to suppose that a very complex muscular apparatus exists, but the anatomical investigation of the parts does not reveal any muscles capable of giving rise to all the wing movements; we scarcely find any but elevators and depressors of the wing.' These observations show how profoundly ignorant this distinguished physiologist was of the complex character of the wing-joint, and of the numerous muscles by which it is moved.

The number of vibrations made by the wings was demonstrated graphically on a revolving smoked cylinder by Marey. He found that in the house-fly the wing makes 330 complete vibrations in a second, and gives the following as the number of vibrations per second in several insects. The wings of the drone-fly make 240 vibrations; of the bee, 190; of the wasp, 110; of the humming-bird hawk-moth (*Macroglossa stellatarum*), 72; of a dragon-fly, 28; and of a butterfly, 9. Marey and Landois\* state that it needs 330 to 340 electric shocks per second to produce tetanus in the wing muscles of an insect, hence it may be concluded that 300 separate contractions may occur. Such rapidity of action appears almost incredible, but it must be remembered that the wings represent the long arms of levers which are moved by very minute changes in the convexity of the dorsum of the thorax.

Lendenfeld's memoir [93] on the flight of the Dragon-flies is

\* Landois, 'Physiology,' translated by Stirling, vol. ii., p. 715.

most exhaustive. He gives an elaborate description of the wings and wing-joints. The structure of the wing-joints and the mechanism by which they are moved differs entirely from that observed in the Coleoptera, Lepidoptera, Hymenoptera, and Diptera. In the Dragon-flies the great wing muscles, as was long ago observed by Meckel and Chabrier, are inserted directly into the wing roots, and not into the thoracic wall. Except in the existence of three roots to each wing, I have been unable to compare the structures exhibited in the Dragon-flies with those of other insects; and the nomenclature employed by Lendenfeld is special. He makes no attempt to compare the wings of the Dragon-flies with those of other insects. Three sets of muscles are, however, found to each wing, corresponding with the three wing-roots.

Lendenfeld took instantaneous photographs of the wings in motion, and claims an exposure of  $\frac{1}{2000}$  of a second. From a series of such photographs he has constructed a projection giving the curves described by the wings. The curve is similar to the one I have given (Fig. 36), but he has reversed the direction of the motion. So far as I can judge, there was nothing in Lendenfeld's method to determine the direction, and in a curve given by him [93, p. 368] he apparently agrees with me completely, not only in the direction of movement, but—if the arrows are reversed in his large diagram to correspond with those given in this curve—in the rotations of the wing plane. The curves are constructed from photographs of the wings of *Agrion puella*.

Lendenfeld, like myself, rejects Marey's theory of passive rotation. He has amplified Marey's tables, giving the relative wing surface in birds and insects. His results show that the wing surface in insects is from twenty to a hundred times greater than in birds for equal body weights. This relation enables the insect to compete with a bird in actual as well as in relative velocity. Leeuwenhoek's old observation on the relative velocity of a swift and a dragon-fly, in which the insect outstripped the bird, is well known and often quoted.

The small sclerites of the wings have been described by Jurine in the Hymenoptera [71], by Chabrier in various insects [72], and by Straus Durckheim [40] in the cockchafer. The descriptions are not in all cases clear, and it is difficult always to recognise the parts indicated. The following are the most important synonyms:

**Parapteron**, Audouin. Claviculaire, Chabrier. Petit radial, Jurine [72, vol. viii., p. 73].

**Pre-epaulet**, Straus Durckheim.

**Epaulet**, Straus Durckheim.

**Coracoid**, Mihi. Bec de l'humérus, Chabrier [72, vi., pl. 18].

**Unguiculus**, Mihi. Base de l'humérus, Chabrier in cockchafer. Ongulaire, Chabrier in Hymenoptera. Petit cubital, Jurine [72, vol. viii., p. 73].

**Dens**, Mihi. Omoplate and sigmoidea united, Chabrier. Grand and petit huméral, Jurine. The sclerite called sigmoidea only occurs, according to Chabrier, in the Hymenoptera. It is evidently a part of the dens [72, vol. viii., p. 73].

**Remigium**, Mihi. Tige basilaire de l'humérus, Chabrier. Chabrier figures the hypopterygium of the cockchafer, but does not mention it in the text [72, vol. vi., pl. 18].

## 5. THE EXO-SKELETON OF THE ABDOMEN.

### a. General Morphology.

The exo-skeleton of the abdomen is as remarkable for its great simplicity and similarity of structure in all insects, as that of the thorax is for its complexity and diversity.

The abdominal skeleton consists of a series of annuli, of which the typical number is nine, except in the Orthoptera, where there are eleven. The ninth is frequently either rudimentary or absent in the imago, its place being taken by a small triangular dorsal plate, very similar to the telson of a Crustacean.

Several, commonly the three last, segments are invaginated and withdrawn within the segment in front of them, and form a cloacal pouch, or a tubular ovipositor. This arrangement reduces the visible external segments in many of the Diptera to five, and the first of these is not always apparent without dissection.

Each annulus of the abdominal skeleton consists of a dorsal arch and a ventral plate.

True paired appendages arise from the ventral plate of the

seventh segment in the male, and a second pair lie one on each side of the dorsal plate of the ninth segment; but neither pair is segmented in the Diptera.

In the female a single pair of leaf-like appendages exist at the end of the ovipositor on the ventral surface of the triangular dorsal plate of the ninth segment.

#### **b. The Abdominal Skeleton of the Blow-fly.**

Eight distinct annuli are present in both sexes, with a triangular dorsal plate, the epipygium, representing the ninth in the female. The epipygium is a deeply-cleft style-like organ in the male.

The five anterior annuli form a pyriform capsule in both sexes, each overlapping the one behind it, so as to protect the soft syndesmotic membrane uniting them; the remainder are invaginated within the fifth. These form a cloaca in the male and a long ovipositor in the female, the sixth, seventh, and eighth segments being drawn one within the other when the organ is at rest.

The first abdominal annulus is very narrow, and its external surface looks forward; so that it is almost entirely concealed by the thorax. Its dorsal arch terminates below in narrow points behind the short, broad ventral plate, so that the syndesmosis between the dorsal and ventral plates is nearly vertical. This syndesmosis contains the first pair of abdominal spiracles.

The second annulus is the largest of all. The lateral portions of the dorsal arch are rectangular, and have the second abdominal spiracles near their anterior angles. The ventral plate of this segment is subquadrate.

The third, fourth, and fifth segments are very similar. The ventral plates become shorter from the second to the fifth. The posterior margins of the fourth, fifth, and sixth segments are fringed with strong curved bristles.

In the male the ventral plate of the fifth segment is deeply incised by a Y-shaped cleft, the edges of which are united by syndesmotic integuments. This arrangement permits of the

extrusion of a part of the seventh and the eighth segments from the cloaca.

The details of the structure and relations of the segments forming the cloaca of the male and the ovipositor in the female and their appendages will be given in the description of the external generative organs.

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## APPENDIX TO CHAPTER V.

### METHODS OF STUDY.

IN the study of the exo-skeleton of an insect the simple microscope is far more useful than the compound instrument, except when the more minute details are in question, and then low powers and a good binocular are most desirable. Except when the parts can be mounted in balsam without pressure, direct light should be used in preference to transmitted.

The slides which are usually prepared and sold as examples of insect anatomy are in general useless, as the parts are crushed and overlap each other.

The microscope which I prefer for use in dissection is Huxley's model, as made for the Normal School at South Kensington, with Zeiss' triplets. These leave nothing to be desired.

For the study of the general structure of the exo-skeleton a number of artificial exuvia should be prepared. I effect this in the following manner: I steep the insects in a five per cent. aqueous solution of caustic soda for a week, or until all the soft parts are dissolved, and then wash them with distilled water. The washing must be very thorough, as even a trace of the caustic soda adhering to the insects' skeletons will destroy them afterwards, or, by forming crystals of soda salts, render the specimens worthless for future use.

In warm weather I find equal parts of alcohol and a ten per cent. caustic soda solution preferable for steeping the specimens, but they need a longer immersion. When the soft parts are

dissolved and the specimens have been well washed, I transfer them to alcohol, in which they may be preserved for years.

Exuvia may be made from insects which have been cut into two or more parts with a razor, and such are the best for studying the interior, as it is difficult to cut the exuvia when made without deforming them.

If it is desirable to bleach the exuvia, this may be done by boiling them for a few minutes in a five per cent. solution of nitro-hydrochloric acid.

In all cases it is necessary to use distilled water only, as the fat of an insect forms insoluble soaps with the lime in hard water, which adhere to the skins and entirely destroy them as specimens.

I examine the exuvia with the simple microscope in a small saucer or watch-glass, and dissect them with fine scissors, after fixing them on a weighted slab of wax or cork with suitable pins.

Before attempting to dissect a skeleton which has been kept in alcohol, it must be transferred to alcohol and water, otherwise it will be too brittle.

The more minute parts are removed by means of the scissors or a fine knife. Knives such as are used by ophthalmic surgeons are convenient, but costly.

The division of the parts can sometimes be effected by tearing the syndesmoses, but it is always safer to cut them through.

The individual sclerites, or groups of sclerites, should then be placed for half an hour in strong alcohol, and afterwards carefully dried at the temperature of the room, and fixed with coaguline upon disc-holders or bristles according to their size.

Disc-holders are small discs of card glued to a piece of cork, through which a pin can be inserted, by which the disc is held in the stage forceps when under observation, and turned in any direction, an essential in examining the sclerites with a compound microscope. Bristles may be fixed to discs with coaguline.

Quekett, in his 'Practical Treatise on the use of the Micro-

scope,' described a very convenient form of disc-holder. A sheet of cardboard is glued on either side of a piece of chamois-leather, and the discs are cut out of this with a sharp punch. One surface should be blackened with Indian ink. The specimens are then fixed to the disc with coaguline. A pin can be thrust through the chamois-leather in any diameter, so that a convenient axis of rotation is easily found, or the axis can be varied at pleasure and the specimen can be turned with precision.

It is always necessary to mount at least two specimens of any sclerite, so that it may be examined on all sides.

It is astonishing how very different the form assumed by a sclerite becomes with even a slight rotation of the disc on which it is fixed, so that it is often a work of hours to determine its real shape when it is examined with the compound microscope.

The smaller sclerites may be mounted in Canada balsam, but must not be flattened by pressure.

I find it best to place the sclerite, or group of sclerites, on a glass slip in a drop of dilute alcohol, and the specimen can then be displayed with needles. This is especially necessary when the minute wing sclerites or the parts of the mouth and other complex organs are required, as otherwise the several sclerites will overlap each other, or assume undesirable positions. When the specimen has been arranged, I remove the alcohol with a small piece of filter-paper, and replace it by a drop of absolute alcohol with a pipette. It is necessary to avoid disturbing the specimen during this process, as it soon becomes hard and brittle, so that it is impossible to move its parts without breaking them. After carefully irrigating the specimen with absolute alcohol, I replace it with clove oil.

Should any turbidity occur in the clove oil, I place the specimen in a warm oven, or gently warm it over a spirit-lamp, when the turbidity will rapidly vanish.

I then drain off the clove oil, place a drop of balsam dissolved in xylol over the specimen, and set it aside under a glass bell. When the balsam is dry, I add a little more, until the specimen is covered with very thick balsam. I then place a

drop of balsam on a cover, and invert it on the object; the thick balsam protects it from the pressure of the cover.

If the object is at all thick, I previously place a small slip of glass of suitable thickness on either side of it to support the weight of the cover.

Mr. Karop, who has mounted some very beautiful specimens, adopts the following method:

His practice is to soak the chitinous parts in weak glycerine—glycerine and water—and to transfer them to stronger solutions of glycerine, and at last to pure glycerine. He makes his cells of Miller's caoutchouc cement, turns a thin layer of the same on the top of the cell, and has a cover smeared with glycerine ready. He then puts the specimen into the cell with more than sufficient glycerine to fill it, but not too great an excess, and turns the cover over it gently, beginning at one edge, and gradually lets it down, so as to drive the surplus glycerine out at the side. This particular cement is not affected by the glycerine, and the glass cover adheres to the cell firmly in a day or two. He then cleans off the surplus glycerine with a brush and water, allows the slide to dry, and turns a ring of cement over the junction of the cell and cover, repeating this in a day or two. Such specimens keep well; some I have are ten years old, and are still perfect.

## CHAPTER VI.

### THE TOPOGRAPHICAL ANATOMY OF THE MUSCLES AND VISCERA OF THE IMAGO (Pl. XI).\*

THE cavities of the head, thorax and abdomen are sharply defined in the adult fly by the narrow apertures of communication between the head and thorax and the thorax and abdomen; but, as has been already observed, the thoracic cavity does not correspond with that of less modified insects, as it is separated from the abdomen by the mesophagma, so that the upper part of the metathorax, much reduced in magnitude, is merged with the abdominal cavity.

The **Cephalic Cavity** is divided incompletely by the tentorium into two parts—an upper portion, which contains the brain, the optic nerves, retinæ of the compound eyes, the compound

\* The intention of the present chapter is to give a brief account of the viscera, and a somewhat more detailed one of the muscular system of the imago. I have purposely avoided all details, and the discussion of doubtful points. My object is to give those who are not familiar with the anatomy of insects the information needful before entering upon a consideration of the developmental history of the embryo and the imago; a knowledge of which will materially assist the student in determining the value of many of the observations, which will find their place in the detailed description of the several organs and systems, to form the subject of a second volume. The seventh chapter of this volume will be devoted to so much of the embryology of the insect in the egg as is involved in the general formation of the body, and will serve as an introduction to the ninth chapter, which will treat of the development of the nymph and the imago, not including the development of the various systems of organs. The eighth chapter will treat of the histology of the tissues; the remainder of this work will be devoted to a detailed description of the several organs and systems of organs; the development of these in the egg, larva, pupa and imago; and, as far as possible, the functions which they perform in the various processes of digestion, secretion, and sensation.

eyes, the median nerve to the ocelli, the ocelli, the antennal nerves, and the frontal sac; and a lower portion, continuous with the cavity of the rostrum, which lodges the fulcrum and its muscles, the commencement of the œsophagus, and the nerves and retractor muscles of the proboscis.

In the adult insect both these cavities contain large air sacs, which occupy the greater portion of them. Those below the tentorium only communicate with those above by a rete mirabile of small convoluted, cylindrical tracheal vessels, which lie in its substance and form the greater part of the membrane in front of the brain. The tentorium itself consists of two cuticular laminæ, separated behind by the œsophagus and the brain, which, although it projects into the upper part of the head cavity, may perhaps be more properly described as lying in the substance of the tentorium; the latter forms its membranous sheath. As, however, the membrane beneath the brain is almost at the same level as the rest of the tentorium, I have preferred to describe the nerve-centres as situated in the supratentorial cavity. It appears to me that the tentorium is in reality a mere thickening of the walls of the tracheal sacs above and below, where they are in apposition with each other, strengthened by the rete of cylindrical vessels already alluded to.

In the imago when it first escapes from the pupa, the tracheal sacs, which eventually occupy so large a portion of the head cavity, are very small, and the greater part of the head is occupied by blood. At this period the frontal sac is everted and forms a large protuberance, also filled with blood.

During the efforts made by the insect to escape from the pupa the frontal sac and head alternately become enlarged with

#### DESCRIPTION OF PLATE XI.

A median vertical section of an adult male Blow-fly :

*a*, antenna ; *cl*, cloaca ; *c s*, chyle stomach ; *d v*, dorsal vessel ; *f*, fulcrum ; *f s*, frontal sac ; *i*, intestine ; *i g*, infra-œsophageal ganglia ; *m*, dorsal muscles (*dorsales*) ; *mm*, leg muscles ; *p s*, pulmonary sac ; *pv*, proventriculus ; *r p*, rectal papillæ ; *s g*, supra œsophageal ganglia ; *s s*, crop or sucking stomach (*honey-bag*) ; *t g*, thoracic ganglion ; *ts<sup>1</sup>*, scutellar air sac ; *ts<sup>2</sup>*, scutal air sac.

[illegible]

MALE BLOW-FLY (vertical median section).



rhythmic regularity. The blood from the head is forced into the frontal sac, and back again into the head capsule. These movements result from the action of a pair of large fan-shaped muscles, which arise from the lower edge of the occipital foramen. Their fibres diverge and are inserted into the genæ and sides of the face; some of these fibres are also inserted into the frontal sac (retractors of the sac), the inner surface of which is covered by numerous muscle-fibres (compressors). Most of these are afterwards absorbed, and in the adult imago they are often entirely absent. The fan-shaped muscles are very conspicuous for a week or more after the insect emerges, but the retraction of the frontal sac takes place within an hour of the escape from the pupa.

**The Cavity of the Thorax** is chiefly occupied by muscles, but there are large air-sacs in the scutum and scutellum, the alar regions, and tympanic bullæ. Beneath the great dorsales, in the axis of the cavity, there is a narrow blood sinus, which contains the thoracic viscera. The following parts are found from above downwards in the middle line in the sinus; the aortic portion of the dorsal vessel, the chyle stomach and proventriculus, the œsophagus, and the thoracic nerve-centre. On either side of the chyle stomach lies the convoluted salivary gland (lingual gland), and externally to this a membranous tracheal vessel, which passes from the head to the abdomen—the paragastric tracheal trunk (Fig. 37).

The sinus is bounded below by the horizontal plates of the entothoracic apophyses, which give origin to numerous muscles.

The anterior process of the scutellum contains a group of chordotonal organs, and the tympanic bulla is filled by a large air-sac connected with the production of the humming sound heard in flight. The halteres also possess complex ganglia and nerve-end organs, and a remarkable group of nerve-end organs lies on the prosternum, the function of which is unknown.

**The Abdominal Cavity** contains two very large air-sacs, the aërostats of Leon Dufour [19], I term them the abdominal

pulmonary sacs; these occupy the whole basal portion of the cavity. The dorsal vessel lies immediately beneath the dorsal integument, within the pericardial sinus; and the posterior extremity of the chyle stomach and the proximal intestine lie in the middle line immediately beneath the pericardium, as far back as the posterior margin of the second abdominal segment; behind this the intestine is much convoluted. Below and behind the pulmonary sacs is the great bilobed crop, which corresponds with the honey-bag of the *Lepidoptera*; when distended it occupies nearly one third of the ventral half of the abdomen.

Behind the honey-bag or crop the sexual glands are seen. They are small in the immature female, but in the adult egg-bearing insect the large ovaries occupy the greater part of the abdominal cavity. The abdominal cavity of the male is much smaller than that of the female, and it is encroached upon by the great sac-like invagination or cloaca, which contains the intromittent organ.

**The Muscular System.**—It is not my intention to describe the individual muscles of the imago in detail, as such a description appears to me to possess little or no morphological interest, and would occupy many pages.

The general arrangement does not differ greatly from that observed by Straus Durckheim [40] in the Cockchafer (*Melolontha*), and Künckel d'Herculais [25] has described the muscles of the genus *Volucella*, which scarcely differ from those of *Musca* in number, origin, and insertion.

It appears to me that the muscles may be conveniently arranged in six groups, in the following manner:

1. Muscles of the head and proboscis.
2. Inter-segmental muscles.
3. Muscles of the wings.
4. Muscles of the legs.
5. Respiratory muscles.
6. Great thoracic muscles.

The first five groups exhibit the same histological structure,

and are termed ordinary striated muscles, or sometimes leg muscles. The sixth group consists of muscles which have a peculiar structure (see Chapter VIII.), and differ entirely from the ordinary form in the Arthropoda; indeed, I know no similar muscles in any group of animals except insects. They are usually known as wing-muscles, or muscles of flight. I prefer the latter term, as there is a group of proper wing-muscles, inserted into the sclerites of the wing-roots, which differ in no respect from the ordinary muscles. Even the term 'muscles of flight' is open to objection, for, although they are only found in winged insects, they are by no means the only muscles of flight; hence I term them great thoracic muscles.

**1. Muscles of the Head.**—The muscles of the proboscis will be described in another section. They are quite unlike the muscles of manducatory insects, and it is, in my opinion, impossible to draw any satisfactory morphological conclusion from a comparison of the mouth muscles of the Diptera with those of the Coleoptera or Orthoptera. The other muscles of the head are referred to in relation to their functions.

**2. Inter-segmental Muscles.**—I have used the term inter-segmental muscles to designate those which form a layer immediately beneath the hypodermis, and which unite the more movable sclerites with each other. They apparently correspond with the integumental muscles of the larva. These are little developed in the head and thorax, but exist in a highly-modified condition in the neck, prosternal region, and between the thorax and abdomen, and form an almost continuous layer on the inner surface of the hypodermis of the abdomen, so similar to the subcutaneous muscles of the larva that the correspondence between the two cannot be doubted.

In the Coleoptera, and in other insects in which the segments of the thorax are mobile on each other, such a layer of muscles is found in a highly-modified condition in the thoracic cavity. Thus Straus Durckheim [40] remarked that the great ventral series of recti muscles, so characteristic of larvæ, are represented successively in the imago of the Cockchafer, from before backwards, by the retractors of the labium, the depressors of the

head, the retractors or depressors of the prosternum, the muscles between the furca of the meso- and metasternum, and the inferior recti of the abdomen, but that the form and size of these is greatly modified, especially in the thorax. In like manner, he adds, the dorsal recti are replaced by the elevators of the head, elevators of the prothorax and scutellum, and the dorsal abdominal muscles.

**3. The Muscles of the Wings.**—Straus Durckheim regards these as part of the inter-segmental system. They are a set of lateral cutaneous muscles, and it is possible they represent the lateral and dorsal inter-segmental muscles of the larva. They are, however, so complex that I have some hesitation in including them in that class, more especially as they are inserted directly into the wing-sclerites. They may be termed elevators, depressors, rotators, and flexors of the anterior and posterior wing-roots. As I have not been able to establish their individual actions, I shall content myself with a short description of the origin and insertion of the principal muscles which act on the wing-roots, merely observing that numerous small fasciculi of muscle fibres are found uniting the various wing-sclerites with each other and with the thoracic wall.

The largest wing-muscle, *musculus lateralis*, is rhomboid in form. It arises from the lateral plate, and is inserted into the long process of the parapteron.

The *musculus accessorius* arises from the dorso-pleural ridge, and is inserted into the parapteron. Both muscles draw the long process of the parapteron forwards and flex the wing in flight (see mechanism of flight, p. 204).

The muscles which arise from the long process of the parapteron appear as a continuation of the *lateralis* and *accessorius*; they are inserted into the sub-epaulet and remigium. A muscle arises from the great ampulla, which is inserted into the dens. This is inserted into a cupule in *Volucella*, and produces rotation of the wing plane according to Künckel d'Herculais [25]. I am unable to adduce any evidence in favour of this view, and am rather inclined to regard it as the elevator of the wing.

The muscles of the posterior wing-root consist of six fasciculi; which arise from the mesothoracic epimeron and the great entopleuron. They converge and form two tendons, which are inserted into the sclerites of the posterior wing-roots; but the exact points of insertion are difficult to determine, as their tendons branch again, and appear to form a plexus with each other. A large branch is inserted into the unguiculus. I have also traced branches of these tendons into various parts of the posterior wing-root.

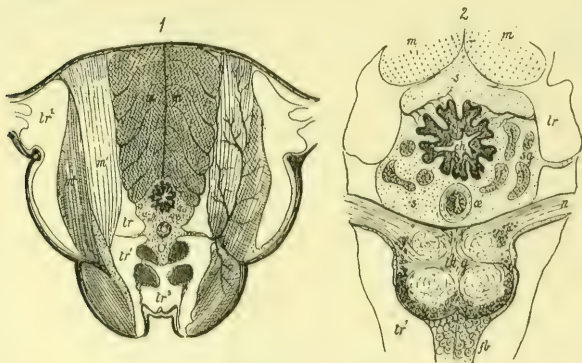


FIG. 3.—1, A transverse section through the mesothorax; 2, a portion of the same, in a more anterior region, to show the contents of the central blood-sinus: *ch*, chyle stomach; *fb*, fat body; *mm*, the dorsales muscles; *m*<sup>1</sup>, sterno-dorsal muscle; *m*<sup>2</sup> *m*<sup>2</sup>, leg muscles; *a*, oesophagus; *n*, nerve-roots; *sg*, salivary gland; *s*, blood sinus; *thg*, thoracic ganglion; *tr*, paragastric trachea; *tr*<sup>1</sup>, descending trachea; *tr*<sup>2</sup>, ascending lateral trachea; *tr*<sup>3</sup>, sternal air-sac.

The gracilis is a curious little muscle with a very long tendon. It arises from the apex of the long process of the parapteron, and is inserted into the parascutal plate.

4. **The Muscles of the Legs** scarcely differ from those of *Melolontha*. The flexor, extensor and abductor of the coxa of the anterior leg, as Hammond observed, arise from the paratrema and epitrochlea. These correspond with the three flexors of Straus Durckheim; there is an adductor which arises from the

great pectoral sclerite. Hammond [78] considers, I think correctly, that the origin of the muscles of the anterior coxa from the paratrema, which he calls the humerus, is an additional argument in favour of its being part of the prothorax.

The corresponding muscles of the two posterior legs are also four in number—one which arises from the lateral region of the tergum, outside the sterno-dorsal muscles; two from the corresponding entothoracic apophyses; and a fourth from the lateral plate of the sternum. Their joint action is circumduction of the limb. There are also several small bands of muscle in the interior of the coxa, the general direction of which is transverse. They are inserted into the trochanter.

The muscles of the femur are a flexor and an extensor. Those of the anterior limbs arise within the coxal joint, which they almost fill; and those of the two posterior pairs of limbs arise from the entothorax, with the coxal muscles.

There is also a flexor and an extensor of the tibia, which arise within the femur; these are bipenniform muscles. A third short bipenniform muscle, the long flexor of the tarsus, ending in a long tendon, also arises high up in the femur. This is inserted into the internal process of the planta, and gives off a slip to the plantar surface of each tarsal joint, which is inserted into the syndesmosis. Straus Durckheim described no corresponding muscle in the Cockchafer, nor do I remember seeing any description of such a muscle in any other insect.

The tibia contains two bipenniform muscles—the flexor and extensor of the first tarsal joint, which are similar to the flexor and extensor of the tibia. There is also a smaller muscle between them, seen in transverse sections. This is perhaps a long extensor of the tarsus, but I have not been able to follow the tendon to its insertion.

There are also short extensors and flexors of the tarsal joints, and of the claws and pads, which extend from each phalanx to the next below. The terminal joint contains the muscles of the claws and pads.

**5. The Respiratory Muscles.**—I have applied this term to the small muscles which control the valves of the spiracles, and

which in some cases also surround the membranous tracheæ, and to certain muscles closely related to the spiracles, to be described hereafter, which I regard as inspiratory.

**6. The Great Thoracic Muscles.**—These are the largest muscles in the insect, and occupy the greater part of the thoracic cavity. They are the dorsales and sterno-dorsales.

The dorsales are six large muscular bands on each side of the median line, which extend from the mesophragma and post-scutellum to the anterior three-fourths of the dorsal shield; they occupy the whole dorso-central region. These muscles are regarded by Straus Durckheim as representing the longitudinal dorsal muscles of the larva of the corresponding segment, and Van Rees believes that he has traced the direct conversion of one into the other in the fly nymph. I shall hereafter give reasons for differing from Van Rees in this respect.

As Hammond [78] has pointed out, the dorsales in the fly are entirely mesothoracic. In many insects both a meso- and a metathoracic set are developed. In the Bees the latter are quite rudimentary, and occupy the interior of the post-scutellum. In the Coleoptera the meta- and not the mesothoracic set are the only ones developed.

The sterno-dorsales are three large bundles of muscle fibres, which extend from the lateral regions of the dorsum to the meso-sternum, and one which extends from the dorsum to the ridge above the posterior spiracle, on each side. These muscles are external to the dorsales in position; their direction is from above downwards, and from before backwards. They are usually regarded as the antagonists of the dorsales (see p. 187). In the Dragon-flies (*Libellulæ*) there are eight sets of these muscles, four in the meso- and four in the metathorax, and they are inserted directly into the wing-roots by cupules, or cup-shaped apodèmes, which terminate in rods attached directly to the wing-sclerites. In all other insects they are inserted into the dorsum, and not into the wing-roots. As in the case of the dorsales, it is apparent, therefore, that all these muscles in the Blow-fly belong to the mesothorax.

It is very generally admitted that the great thoracic muscles are the most powerful agents of flight, and that they act upon the wings by altering the convexity of the dorsum, and its relation to the mesosternum which supports the wings through the intervention of the pleural plates. It is generally believed that the dorsales depress and the sterno-dorsales elevate the wings.

I have already stated (p. 187) that it does not appear that the two sets of muscles are direct antagonists, nor is it apparent why the elevators of the wings need to be as powerful as the depressors. The latter movement raises the whole weight of the insect, whilst the elevation of the wing does no work in flight, but only prepares it for the downward stroke. I think it more probable that the sterno-dorsales give power to the back stroke, and urge the insect forwards. The wing-joints and their relations to the thorax are so complex that it is not easy to ascertain exactly the movements of the wing each slight alteration of the position of the parts produces, as these depend upon the angles which the articulating surfaces make with each other.

**The Respiratory Organs.**—The tracheæ of the head and thorax, with the exception of their smaller branches, are all membranous sacs; those of the abdomen, except the great air-sacs at its base, are all cylindrical vessels, which exhibit a spiral arrangement of the intima. The existence of membranous tracheæ and dilated tracheal sacs is characteristic of all aerial insects, but I know no other group in which the cylindrical tracheæ are more completely replaced by thin-walled tubes of variable calibre than the Muscidæ and the allied Diptera.

It is usually stated that the air is forced out of the tracheal vessels by the contraction of the abdominal muscles, and that they are refilled by the elasticity of the spiral thread in their walls. Such an explanation is totally inadequate to explain the filling of the tracheæ with air in the Diptera, where the sacs have no tendency to expand—indeed, they collapse as soon as an opening is made for the escape of air; neither is there any tendency for the abdomen to expand by the elasticity of its

integument, and it is not possible that any muscular contraction can bring about this result. As the large spiracles are thoracic, it might be supposed that the expansion of the thorax acts as an inspiratory agent; but no such expansion occurs. The only possible way in which such an expansion could occur is by the cavity being rendered more spherical by the contraction of the dorsales muscles, without any alteration of the extent of its surface, as it is well known that a spherical envelope encloses a maximum space; but the contraction of these muscles closes the syndesmoses, and renders the surface smaller, so that there is no reason to believe that the size of the cavity can be increased by their contraction. I shall hereafter show that the mechanism of inspiration is entirely independent of either thoracic or abdominal movements, and that the air is pumped into the tracheæ by a special mechanism.

The general arrangement of the tracheæ in the larva has been already described, and this appears to be the ground-form of the tracheal system. In the Blow-fly imago this ground-form still persists, but is masked by the complexity of the branches, which are often larger than the longitudinal trunks.

The vessels which represent these lie one on either side of the thoracic blood-sinus (Fig. 37)—these I term the paragastric trunks. The paragastric tracheæ enter the head as narrow vessels, one on either side of the neck. Each immediately gives off a branch which passes below the jugum and tentorium, and dilates to form the air-sacs of the proboscis; the main trunks then unite and form a single median vessel, which ascends on the posterior surface of the brain; its walls are greatly thickened, it gives off lateral branches to each side, and terminates above the brain by dividing into two again. The branches of this vessel dilate in front of the brain into the air-sacs of the supra-tentorial region of the head.

The paragastric trunks are connected with the anterior and posterior spiracles by transverse or spiracular trunks, and immediately behind those from the posterior spiracles they become very narrow, pass beneath the mesophagma, and enter the great abdominal pulmonary sacs, which form the

posterior part of the paragastric system. The paragastric trunks are united with each other immediately in front of the mesophagma by a large transverse vessel, and again opposite to the anterior spiracles in front of the chyle stomach and proventriculus. The paragastric vessels give off numerous branches which ascend between the dorsales and sterno-dorsales; these ramify, and form a network between all the adjacent muscles.

The sternal air-sacs are very large, far larger than the paragastric trunks. They receive their air from the sacs which unite the paragastric trunks, and therefore directly from the spiracles, which are connected with the paragastric trunks where they give off their commissural branches. The sternal air-sacs supply the intermediate and posterior limbs and their muscles.

The anterior limbs are apparently supplied by the branches of the anterior spiracular trunks, which exhibit many voluminous offsets, supplying the anterior part of the thorax and the wing-muscles.

The posterior spiracular trunks give off the largest thoracic air-sacs. These ascend and supply the scutal and scutellar air-sacs, the great air-sacs of the tympanic bulla, and the air-sacs of the wing-root; they are connected with the expiratory tympanic spiracle, the auditory apparatus, and the organs of sound, as well as with the sacculus and hypoptergium. A chain of small air-sacs between the sterno-dorsales and the muscles of the legs unite the anterior and posterior spiracular trunks; it is parallel with the paragastric trunks. All these vessels give off numerous branches, which end in cylindrical tracheæ, and these again in tracheal capillaries.

The tracheæ of the abdomen are arborescent cylindrical vessels; they arise from the spiracles of the third, fourth, and fifth segments. Those of the first and second segments communicate with the pulmonary sacs by short membranous tubes. I have been quite unable to find any longitudinal trunks uniting the vessels from the posterior abdominal spiracles, which appear to form a separate system, only connected with the

vessels from the great air-sacs by capillaries or small branches. They are chiefly distributed to the integument, the generative organs, and the posterior part of the intestine. The great tracheæ of the intestine are derived from the pulmonary sacs.

In the Hymenoptera (*Bombus*, Newport [9]) the great longitudinal vessels, represented in the Fly by the paragastric trunks and abdominal sacs, form connecting longitudinal commissures behind the abdominal air-sacs, between the tracheæ arising behind the second abdominal spiracles, and terminate by uniting with each other in the last abdominal segment. It will be seen that the discontinuity of the longitudinal air-trunks and the vessels arising from the posterior abdominal spiracles is dependent on the very peculiar arrangement of the larval spiracles in the Muscidæ, and is of high developmental significance (see Development of the Tracheal System).

**The Alimentary Canal** of the imago differs from that of the larva in the highly-modified form of the mouth, the ventral position of the crop, in the presence of highly-developed glandular organs in the rectum, the rectal papillæ, and in the great shortening of the distal intestine, or that portion intervening between the Malpighian tubules and the rectum. The following are the comparative measurements of the intestine in the larva and imago:

				LARVA.	IMAGO.
Chyle-stomach and proximal					
intestine	...	..	...	15 mm.	19 mm.
Distal intestine		...	...	34 mm.	4 mm.
Rectum	...	...	...	1 mm.	2 mm.
				<hr/>	
Total length	...	...	...	50 mm.	25 mm.

The long appendicular cæca of the chyle-stomach of the larva are absent in the imago, but the wall of the chyle-stomach is alveolar, the alveoli undoubtedly representing the glandular cæca with which the chyle-stomach is covered in many insects. The greater part of the intestine forms a spiral coil, which is situated in the dorsal region of the abdomen, behind the pulmonary sacs and above the sexual glands. The details of structure

will be treated of in a special chapter, in which the functions and morphology of the several parts will be fully considered.

The salivary lingual glands are long convoluted tubes, which, as already stated, lie one on each side of the chyle-stomach in the thorax. They are prolonged into the abdomen, lying at first on either side of the proximal intestine, and then beneath intestinal coil; they terminate just in front of the rectum.

The large folliculate salivary glands, accessory glands, so frequently present in insects, are entirely wanting; but a pair of small folliculate glands are found in the oral disc of the proboscis, the ducts of which open on its oral surface, and there is said to be a pair of minute glands at the proximal extremity of the fulcrum (Kraepelin); I have, however, been unable to establish the glandular structure of these, and am inclined to believe they are merely minute fat bodies.

**The Nervous System** in the Muscidæ is greatly concentrated: not only are the supra- and infra-œsophageal nerve-centres united into a single complex mass, which I term the brain, but all the remaining ventral ganglia are united in one centre—the thoracic nerve-centre. There is also a proventricular ganglion, corresponding with the proventricular ganglion of the larva, which is united with the crura of the supra-œsophageal ganglia by a median, stomogastric, nerve. The visceral nerves arise from the proventricular ganglion. There is no frontal ganglion lying, as is usual, in front of the brain, but it is probable that the nerve-cells on the inner surface of the crura of the supra-œsophageal nerve-centres, from which the stomogastric nerve arises, represent it.

The structure of the nervous system is exceedingly complex, and will be fully treated of in a separate chapter; and the origin and distribution of the somatic and stomogastric or visceral system of nerves will also be more conveniently considered hereafter. I will only add in this place that the brain is apparently concerned in the reception of impressions derived from the various sensory organs of the head, in the movements of the proboscis, and in the initiation of such movements as may be regarded as of an automatic, rather than a reflex, character.

The thoracic ganglion appears to represent functionally the medulla oblongata and spinal cord of vertebrates. Its destruction causes instant death, whilst a fly from which the head has been removed behaves very much as a vertebrate does after the removal of the cerebral hemispheres. It is worthy of remark that the great nerves to the halteres, which also supply the chordotonal organs of the thorax, are connected with the thoracic nerve-centre, just as the auditory nerves of vertebrates are with the medulla oblongata.

The organs of the special senses and the complex sexual apparatus cannot be considered in this part of my work, as it will be necessary to give full details of their structure and development to justify the views I hold, and a brief account of these parts would be practically without value.



THE FEMALE BLOW-FLY (*Calliphora Erythrocephala*).

## CHAPTER VII.

### THE EMBRYOLOGY OF THE BLOW-FLY IN THE EGG.

#### 1. EARLY CHANGES IN THE OVUM SUBSEQUENT TO FERTILISATION AND FORMATION OF THE BLASTODERM.

NOT only is the metamorphosis of the Diptera comparable with that of Echinoderms and Nemertids, but the earlier stages of development in the egg are exceedingly similar.

#### Bibliography:—

96. ZADDACH, G., 'Ueber die Entwicklungsgeschichte des Phryganiden Eies.' Berlin, 1854.
97. KOWALEVSKI, A., 'Embryologische Studien an Würmern und Arthropoden.' Mem. Acad. Imp. Sci. St. Petersbourg. Ser. 7, tom. xvi., 1871.
98. METSCHNIKOFF, E., 'Embryologie des Scorpions.' Zeitsch. f. w. Zool., Bd. xxi., 1871.
99. BOBRETZKY, N., 'Ueber die Bildung des Blastoderms und der Keimblätter bei den Insecten.' Zeitsch. f. w. Zool., Bd. xxxi., 1878.
100. WEISMANN, A., 'Beiträge zur Kenntniss der ersten Entwicklungsvorgänge im Insecteneies, in: Beiträge zur Anatomie und Embryologie, J. HENLE von seinen Schülern als Festgabe dargebracht.' Bonn, 4to, 1882.
101. SELENKA, E., 'Studien über Entwicklungsgeschichte der Thiere. Heft ii., Die Keimblätter der Echinodermen, 4to, Wiesbaden, 1883 (with six plates).
102. WITLACZIL, E., 'Entwicklungsgeschichte der Aphiden.' Zeitsch. f. w. Zool., Bd. xl., 1884.
103. KOROTNEFF, A., 'Die Embryologie der Gryllotalpa.' Zeitsch. f. w. Zool., Bd. xli., 1885.
104. KENNEL, J., 'Entwicklungsgeschichte von Peripatus Edwardsii,' etc. Arb. d. Zool. Zoot. Inst., Würzburg, Bd. vii. und viii., 1885-88.
105. KOWALEVSKI, A., 'Zur Embryonalen Entwicklung der Musciden.' Biol. Centralblatt, Bd. vi., 1886.
106. BRUCE, A. T., 'Observations on the Embryology of Insects and Arachnids.' Baltimore, 4to, 1887.
107. BLOCHMANN, 'Ueber die Richtungskörperchen bei Insecten. Morph. Jahrbuch.' Bd. xii., 1887.

In the Diptera, as in the Echinodermata, there is a blastula stage. The blastoderm at this period is a closed vesicle consisting of a single layer of cells, which only differs from the echinoderm blastula in the abundant food-yolk which it contains.

If the views which I have adopted are correct, in both cases there is a total segmentation of the germ-yolk, and the archenteron is developed by an invagination of the blastoderm—gastrulation—whilst the mesoderm in both is developed by a pair of diverticula, originating from the hypoblast, in close proximity to the original blastopore, which eventually surround the archenteron. In the Muscidæ, and in some Echinoderms, *Echinus*, the definitive anus is developed as a distinct involution of the epiblast, and the blastopore is closed before the proctodæum comes into relation with the archenteron; moreover, in both the greater part of the wall of the original

108. WILL, L., 'Entwicklungsgeschichte der Viviparen Aphiden.' Spengel's Zool. Jahrbuch. Abth. f. Anat. u. Ontog., Bd. iii., 1888.
109. BÜTSCHLI, O., 'Bemerkungen über die Entwicklungsgeschichte von Musca.' Morph. Jahrbuch, Bd. xiv., 1888.
110. VOELTZKOW, P. A., 'Vorläufige Mittheilung über die Entwicklung im Ei von Musca Vomitoria.' Zool. Anzeiger, n. 278, 1888.
111. VOELTZKOW, P. A., 'Entwicklung im Ei von Musca Vomitoria.' Arbeiten aus dem Zool. Zoot. Inst. zu Würzburg, 1889.
112. VOELTZKOW, P. A., 'Melolontha Vulgaris.' Ein Beitrag zur Entwicklungsgeschichte im Ei bei Insecten. Arbeiten aus dem Zool. Zoot. Inst. zu Würzburg, 1889.
113. CHOLODKVOSKY, N., 'Studien zur Entwicklungsgeschichte der Insecten' (Blatta Germanica). Zeitsch. f. w. Zool., Bd. xlviii., 1889.
114. GRABER, V., 'Vergleichende Studien über die Embryologie der Insecten und insbesondere der Musciden.' Denkschrift, K. Akad. Math. Naturwissen Cl. Wien., Bd. lvi., 1889.

This work consists of 58 pages of letterpress, illustrated by 10 plates, and is the most complete work on the subject extant. It contains an extensive bibliography.

115. GRABER, V., 'Vergleichende Studien am Keimstreif der Insecten.' Denkschrift K. Akad. Math. Naturwissen Cl. Wien. Bd. lvii., 1890.

This work consists of 113 pages of letterpress, illustrated by 12 plates. It is an epoch-making work on the embryology of insects. The bibliography appended gives references to 82 memoirs on the subject.

blastocoele forms only temporary structures—the echinopædia or ciliated embryo in the one, and the membranes the serosa and amnion in the other.

**Centrolecithal Yolk Segmentation.**—It is indubitable that cells, or according to some nuclei, appear in the interior of the yolk in Arthropods generally, and that these travel to its periphery, and it is further believed that those which arrive first at the surface of the yolk unite and form a single layer of cells, the ectoblast, over its whole surface, and that others which remain within the yolk form the hypoblast. The cells which appear in the interior of the yolk are stellate and amœboid, whilst the blastoderm itself consists of epithelial elements. The manner in which these epithelial elements are

#### DESCRIPTION OF PLATE XII.

Embryological studies of various Insects after Graber. (All the figures except FIG. 12 are from his last memoir, 115.)

FIG. 1.—A median section of a six-days-old egg of the Burnet Moth (*Zygana filipendula*); showing the relations of the embryo and membranes to the yolk in the endolecithal type.

FIG. 2.—A transverse section of the egg of a field Cricket (*Stenobothrus variabilis*); showing an early stage of an embryo of the epilecithal type.

FIG. 3.—An egg of *Stenobothrus*, showing a young embryo.

FIG. 4.—A more advanced egg of the same insect.

FIG. 5.—The isolated primitive band of a butterfly, *Pieris Crategi*, from the egg on the fifth day.

FIG. 6.—The primitive band of the same on the sixth day.

FIG. 7.—A transverse section through the anterior part of the primitive band of the Burnet Moth (*Zygana filipendula*), showing the amnion.

FIG. 8.—A surface view of the egg of a beetle, *Lina tremula*, on the second day.

FIG. 9.—The embryo of the same removed.

FIG. 10.—The head of the embryo of the butterfly, *Pieris Crategi*, on the seventh day.

FIG. 11.—Section through the first abdominal segment of a *Stenobothrus* embryo, showing the coelomic sacs. (The right side is segmental the left intersegmental.)

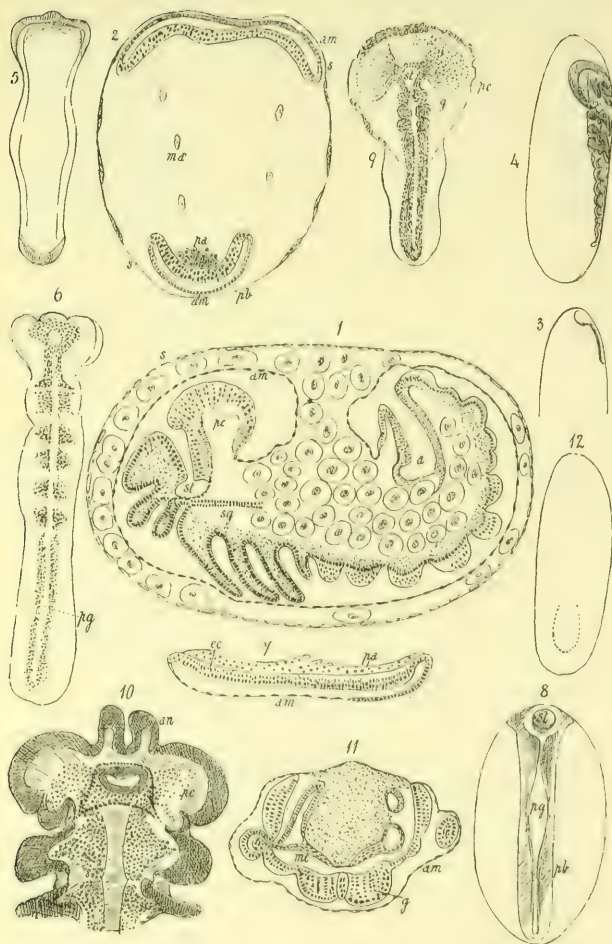
FIG. 12.—A diagram of the egg of the Blow-fly before the blastoderm appears on the surface of the yolk.

The dotted line shows the position and form of the blastoderm at an early stage of development. This diagram was constructed by Graber from a series of sections, and is given in his memoir on the fly embryo (114, page 140).

The following references apply to all the figures in which they occur :

*a*, archenteron, Mihi (*proctodeum*); *am*, amnion; *an*, antenna; *g*, ganglia; *me*, mesamœboids of the yolk; *me*, mesoblast, or wall of the coelomic sac; *pa*, parabolic-layer; *p b*, primitive band; *p c*, procephalic lobes; *p g*, primitive groove; *s*, serosa; *s g*, salivary duct; *st*, stomodæum.

PLATE XII.





developed from the amœboid yelk-cells is unknown, if indeed any such transformation occur. Most embryologists suppose that the yelk-cells are derived from the segmentation of a nucleus, the germinal vesicle, which pre-exists in the egg, or to use a more modern nomenclature, from a pronucleus derived from the germinal vesicle. As the first cellular elements appear to travel from the interior towards the surface of the yelk, the process has been termed centrolecithal segmentation.

**Origin of the Blastula.**—Korotneff [103] says, with regard to the formation of the blastoderm in *Gryllotalpa*: ‘According to Weismann [100], the cells of the blastoderm are formed in the interior of the egg, and pass outwards to the surface of the yelk, but are widely separated from each other, and multiply subsequently by fission until the blastoderm is closed. According to my observations this process occurs as Weismann describes it’ (p. 571).

This is the generally accepted theory of the manner in which the blastoderm is formed by centrolecithal segmentation. Its improbability lies in the supposition that the centrolecithal segmentation cells are formed from the germinal vesicle, and that, after passing through a stage as separate amœboid wander cells, they subsequently unite and form the blastoderm. Korotneff continues: ‘I have not been able to observe the origin of the first cell from the germinal vesicle, but do not doubt the possibility (*Möglichkeit*) of such an origin. The first cells are not large, are amœboid, and are four or five in number; they pass to the surface of the yelk, and then undergo considerable enlargement.’ He adds: ‘Such cells on the surface of the yelk resemble parasitic amœbæ. In the second generation these cells become multinucleate.’

With regard to the formation of the blastoderm itself, Korotneff says: ‘It first appears on the ventral surface of the egg in the form of numerous white specks. When we investigate one of these, we incline to the opinion of Bobretzky that they are intermediate between the amœboid cells and the elements of the blastoderm; they are entirely without nuclei.’ It is from these that Korotneff believes the blastoderm is

developed, but this is the hiatus which has not hitherto been bridged over by observation. No one has actually seen the process by which these are converted into epithelial elements.

The white specks without nuclei, which Korotneff speaks of, have long been observed. Zaddach [96] described them as a number of clear vesicular spots, and Leuckart [20] says of them: 'I must hold it as an error when it is maintained that they are nucleated cells, and therefore the same which ultimately form the blastoderm. These clear flecks are present only in small numbers, and are separated from each other by considerable spaces; they are transparent, without nuclei, and with a doubtful investing membrane, so that they may easily be taken for drops of sarcode.' And he repeats: 'The clear flecks which appear after fertilisation in insects' eggs, and without exception in the peripheral substance of the yolk, are not cells, but rather bodies which lead to cell formation.' That Leuckart in 1858 should have held such a view is not astonishing, but that it should still be entertained seriously is incomprehensible to me. The production of a cell from a clear speck without a nucleus, a mere vacuole, and possibly a *post-mortem* appearance, is at variance with all that is known regarding cell-formation, and I should have thought identical with the spontaneous generation of cells.

The presence of stellate cells within the yolk in Arthropods, which multiply with great rapidity before the blastoderm makes its appearance, is an undoubted fact, but the supposition that they are formed from the female pronucleus, or from the germinal vesicle, and that they ultimately become the epithelial blastoderm, is a theory which, in my opinion, is not supported either by what happens in other forms of animal life, or by any direct observations. Precisely similar cells make their appearance in the interior of the fat bodies, and result from the division and subdivision of the original cells in which the fat is deposited (see Chapter VIII.), and I have long held that the centrolecithal cells are mesamæboid or parablast cells.

**The Parablast.**—Until quite recently all the tissues of the body in every form of the Metazoa were supposed to originate

directly from the germinal layers of the blastoderm; lately, however, most embryologists have adopted the view which originated with His, that the blood and the connective tissues—in insects the connective reticulum and the fat bodies—arise from amœbiform cells (mesamœboids), called by His parablatic, and by the brothers Hertwig mesenchymatous cells. According to R. and O. Hertwig [119] ‘very little is known of the origin of the mesenchyme; it can only be said that in different classes of animals it originates from different sources, and appears at various stages of development, but once formed, it penetrates between the epithelial laminae of the blastoderm and the tissues arising from them, investing, uniting and supporting them.’ It consists of cells arranged in no definite order, and separated from each other by a copious intercellular matrix.’

His, as long ago as 1865 [116], was led to regard the blood and connective tissues of the chick as developed from cells which originate in the great food-yolk, which he believed to wander in between the layers of the blastoderm. These in-wandering cells he termed parablats. I have frequently myself seen numerous amœboid cells in the yolk of a bird’s egg in the early stages of incubation. The above view of His met with little acceptance for a long time, and he subsequently

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**Bibliography.**—Those who are interested in following up the views of His and Hertwig further should consult the following works :

116. HIS, W., ‘Die Häute und Höhlen des Körpers.’ Basle, 1865.
117. HIS, W., ‘Der Keimwall des Hünereies und die Entstehung der Parablatischen Zellen.’ *Zeits. f. Anat. und Entwicklungsgeschichte*, 1876.
118. HIS, W., ‘Unsere Körperform und das physiologische Problem ihrer Entstehung. Briefe an einen befreundeten Naturforscher.’ Leipzig, 1879.
119. HERTWIG, O. and R., ‘Die Cœlomtheorie. Versuch einer Erklärung des mittleren Keimblattes.’ Jena, 1881. 8vo. *Studien zur Blättertheorie*. Heft iv.
120. HIS, W., ‘Die Lehre von Binde-substanzkeim (Parablast). Rückblick nebst kritischer Besprechung einiger neuerer entwicklungsgeschichtlicher Arbeiten.’ *Archiv f. Anat. und Phy. Anat. Abth.*, 1882.
121. WIELOWIEJSKI, H., ‘Ueber das Blutgewebe der Insecten.’ *Zeitsch. f. w. Zool.*, Bd. xliii., 1886.

modified it, regarding the parablast cells as originating from the edges of the newly-formed blastoderm.

Quite recently Wielowiejski [121], so far as insects are concerned, has returned to the original view of His. He says: 'I have traced the parablast cells directly to the segmentation spheres of the yolk.' Most embryologists trace the parablast to the blastoderm itself, and in cases where there is no large food-yolk it is difficult to see what other origin it can have; but where a large food-yolk is present, it seems to me that its origin from the yolk is probable, and in insects I believe it is formed from the centrolecithal segmentation cells.

Although Graber and others trace the development of the fat bodies and other connective tissues to the epiblast, it appears to me that the evidence in favour of this view is such that it is equally favourable to that which I have adopted. Moreover, there is strong reason to believe that the mesenchymatous tissues of the imago are not developed from the imaginal discs, but originate from the immigrant blood cells of the larva and the stellate cells of the tracheæ, as Viallanes and Künckel d'Herculais maintain; whilst the muscles, which represent the true mesoblast, originate directly from the disc epiblast, as Ganin insists. If this is so, then analogy is in favour of the origin of the connective tissues of the embryo from the undifferentiated yolk-cells, rather than from the specialised epithelium of the blastoderm.

**The Relation of the Germ to the Vitellus.**—The ova of the metazoa either consist of a germ-yolk which undergoes equal segmentation, *holoblastic ova*; of a germ which is loaded by food-yolk in which segmentation is unequal; or of a germ which undergoes complete segmentation, and a yolk which either does not segment at all or in which the segmentation, if it can be called segmentation, takes place at a later period when the morula produced by the segmenting germ is already converted into a blastoderm, entirely or partially, surrounding the yolk; which is subsequently absorbed in the nutrition of the embryo.

It is well known that in many of the Vermes the germs are developed in one gland and the yolks in another, and that the yolk and germ are only united during their passage through the oviduct.

I have shown elsewhere\* that there is the strongest evidence, in my opinion, that in the fly the germs and yolks are developed in separate follicles, and that the germ passes into the vitellus immediately before the egg is impregnated and during its passage through the oviduct.

The evidence upon which this view rests depends upon the developmental history of the ova and on the structure and contents of the internal generative organs of the female insect. The facts upon which I base my hypothesis that in the Fly, and in Insects generally, the germ is developed separately from the food-yolk and passes into it before the sperm, will be given hereafter, and for the present I must refer my readers to my published work on the subject already cited.

I would only observe in this place that the ova of the Echinodermata are holoblastic, and that food-yolk is entirely, or almost entirely, absent, so that the segmentation is absolutely regular and equal; that in the viviparous *Peripatus*, according to Kennel,† the germ is without yolk, and undergoes equal segmentation; that in the viviparous Scorpions the germ is formed before the yolk, and undergoes regular segmentation; and in the parthenogenic Aphides segmentation of the germ precedes the formation of the yolk.

If my contentions on this subject are correct, it follows that segmentation, homologous with that of the Echinoderm, can only affect the minute germ-yolk, whilst the food-yolk must be regarded as a store of food material, which takes no part in the

\* 'On the structure and development of the ovaries and their appendages in the Blow-fly.' 'Journal of the Linnean Soc. Zool,' vol. xx., 1889, pp. 418-442.

† SYNCYTIAL SEGMENTATION.—The phenomena described in *Peripatus* as syncytial segmentation, appear to me to be due to imperfect fixation; in my earlier investigations I had numerous sections of Blow-fly embryos which presented precisely the appearances figured by Sedgwick, which I subsequently learned to be delusive. (Compare Kennel [104].)

production of the blastoderm, except that it serves to nourish the growing morula formed by the segmenting germ, but which, nevertheless, is directly concerned in the development of the parablast—in other words, which may be regarded as a part of the mother organism, by which the germ is nourished.

Theoretically, according to this view, the parablast might be regarded as of parthenogenetic origin; but it must be remembered that the parablastic cells would probably be affected by the growth of the morula, and the second or third generation of amœboid parablastic elements may possibly become more or less modified by the male parent. That parthenogenesis exists in insects is well known, and it may be that the origin of the parablast directly from the mother is a relic of true parthenogenesis.

**The Polar Cells of Weismann.**—In the Diptera, more especially in *Chironomus*, the polar cells of Weismann actually exhibit the same segmentation phenomena as the holoblastic ovum, and I believe they represent the vegetative pole of the morula, which results from the segmentation of the germ-yelk. Weismann [2] described these cells in the egg of *Chironomus*, which is exceedingly favourable for their observation. He says: ‘In the youngest eggs I have observed that the yelk is covered by a highly-refractive bluish layer of germinal blastema (Keimhaut-blastem). At the hinder pole of the egg, in a space between the germinal blastema and the yelk-sac, are four large oval or spheroidal cells, which I term polar cells.’

I would remark that my sections show that the layer of clear yelk substance, which is believed by some to become the blastoderm, exists in the unimpregnated ovarian yelks. It probably represents the white yelk of Birds and Reptiles.

Weismann observed that the polar cells undergo binary division, so that the four cells become 8, 16, and 32 successively. With regard to the polar cells of the Blow-fly embryo, he observes that, ‘although easily overlooked, they conform in their manner of multiplication with those of *Chironomus*.’ I have been unable to detect them until they form a plate of relatively small cells at the posterior pole of the blastodermic

vesicle, exactly as they are figured by Graber [114] (see Pl. XIII., Fig. 2).

I conclude that the earlier cleavage of the polar cells occurs in the Blow-fly during the passage of the germ through the food-yelk. If a young morula is formed as I suggest, it is easy to understand the difficulties which arise in the direct observation of the cleavage of the germ-yelk; and I believe that the morula is easily broken up into its constituent cellular elements, which become scattered in the abundant food-yelk. This view accounts for the segmenting nuclear spindles which have been detected by the laborious researches of Blochmann [107], and others, lying scattered in the food-yelk. If the young morula assumes the form of an open cylinder, as it does in *Synapta*, or is perforated by intercellular openings, as it is in *Echinus* (Selenka [101]), or remains an open cup, it is not difficult to understand the manner in which the food-yelk passes into its interior.

The view that such is the origin of the blastoderm vesicle is directly supported by Graber's figures [114, Pl. VI., Figs. 60 to 67], and by his woodcut on p. 260, which I have reproduced in Pl. XII., Fig. 12. It is true that Graber regards these figures as representing abnormal phenomena, but I regard them as normal, and am at a loss to understand why he considers them abnormal; his only ground for the supposition appears to be that they do not accord well with received views.

Moreover, Metschnikoff's [98] description of the formation of the blastoderm in the Scorpion exactly corresponds, so far as the segmentation phenomena are concerned, with the description I have given above; in these Arthropods at least yelk segmentation is holoblastic, and the yelk grows after the morula is formed. So also in *Peripatus*, if the observations of Kennel are to be trusted—and they certainly appear to be far more trustworthy than those made by his opponents—the yelk segmentation in this group is holoblastic.

In conclusion, I would observe that although the older investigators held that the blastoderm in Insects appears simultaneously over the whole surface of the yelk, more recent

observations indicate that it first appears on the ventral surface, or near the posterior pole of the egg, and gradually extends over it, or that it is at first a small cup-like blastoderm buried in the interior of the yolk, as in the Blow-fly.

Whatever view may be held as to the manner in which the blastoderm originates, all observers agree that in the egg of the Blow-fly, two or three hours after impregnation, it forms a single layer of columnar epithelial cells, enclosing the whole food-yolk. This is the blastula stage. The cells, however, near the posterior pole in the region corresponding with the polar cells are smaller than the rest, and a few of the segmentation cells, resulting from the division of the polar cells, apparently remain adhering to its surface.

**The Gastrula Stage.**—L. Will [108] remarks on this subject: 'There are in the development of insects two stages which may be equally regarded as gastrulation. The first, which I shall term Gastrula No. 1, occurs at a very early period of development. Part of the cells derived from segmentation arrive at the periphery of the yolk, and form the ectoderm; others remain in the yolk, and form the endoderm. The second, my Gastrula No. 2, occurs at a much later period, after the whole egg is enclosed in the blastoderm, and consists in a sinking-in of the middle of the primitive band, so as to form a long median fissure, the median groove (*Keimfurche*, or *Mesodermrinne*).'

I am averse to the use of the term gastrula in either of the senses in which it is used by Will, as neither one nor the other stage represents the gastrula of either an Echinoderm, Mollusc, or Vertebrate in any sense whatever, and the use of the term indiscriminately for either can only lead to serious misconceptions.

True gastrulation gives rise to the formation of an archenteron, bounded by hypoblast. If we compare the stage called by Will 'Gastrula No. 1' with the corresponding stage of the Echinoderm embryo it is clear that the so-called hypoblast is the mesenchyme.

With regard to Will's 'Gastrula No. 2' in the Blow-fly embryo, a ventral invagination of the epiblast certainly occurs; but this

is by no means constant in Insects. I shall hereafter show that it is an extreme modification of the usual process. It has been described by Graber, who speaks of it as the ventral ptychoblast, and he believes that the mesoblast is formed from it. The mesoblast in the fly is not so developed, and I think there can be little doubt that Graber's ventral ptychoblast is in reality the amnion, and has nothing whatever to do with the median groove in the primitive band, and this groove has nothing whatever to do with the formation of the archenteron; therefore whatever view is taken, it cannot be gastrulation.

The very prevalent idea that the median groove in the primitive band of insects represents a blastopore, which originated with Sedgwick, and was supported by Balfour, is very ably controverted by Kennel [104]. It appears to me to be entirely due to a misconception. It is of course absolutely untenable if my conclusions and observations are correct.

## 2. FORMATION OF THE MEMBRANES AND PRIMITIVE BAND.

**The Embryonic Membranes** of insects are an external membrane, termed the serosa, and an internal, the amnion. Similar membranes are also found in other Arthropods, but authors are by no means agreed as to the real nature and homologies of these. In many insects the greater part of the cellular layer enclosing the yelk, the blastula, becomes converted into the membranous coverings of the embryo.

**Relation of the Primitive Band to the Amnion and Serosa.**—In most insects the primitive band (see p. 13) and the rudimentary procephalic lobes appear upon the ventral aspect of the blastoderm before there is any amnion or serosa developed, and the latter are formed either by the sinking of the embryo into the yelk, as in the Lepidoptera, or by the growth of a fold over the ventral surface of the embryo from its edges. In both cases the external layer is termed the serosa, and the internal the amnion. In some insects, as in the Lepidoptera, the yelk passes into the inter-amnial space; in others the yelk is entirely on the dorsal surface of the embryo.

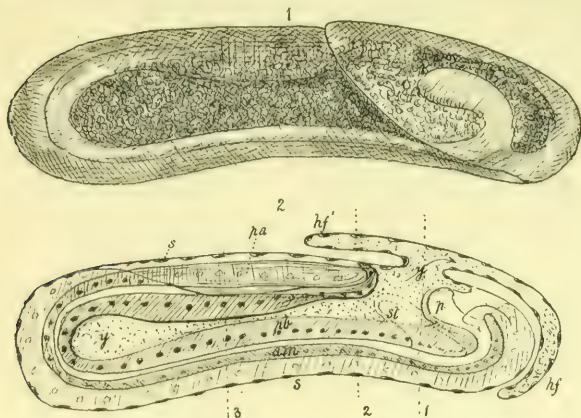


FIG. 38.—1, An Optical Section of an Embryo in the stage represented by sections, Figs 3 to 6, Pl. XIII.; 2, A Diagram constructed from Transverse Sections. The parts surrounding the yolk are drawn larger than they really are, so that the yolk is represented by too small a space: *am*, amnion; *pb*, portion of the amnial tube which becomes the primitive band; *pa*, primitive archenteron; *p*, procephalic lobe; *s*, serosa; *hf*, *hf'*, head-fold. The position of the future stomodæum is represented by the dotted line *st*. The shaded nuclei indicate cells which occupy the median line. The arrow, *y*, shows the communication between the folds of the serosa and the yolk; the second arrow below this shows the opening into the amnial tube in the cephalic region.

#### DESCRIPTION OF PLATE XIII.

The figures in this plate are all copied from Graber [114].

FIG. 1.—A section of the egg of a Blow-fly, showing the segmenting morula within the yolk (a condition regarded by Graber as abnormal).

FIG. 2.—The posterior pole of the blastoderm of the Blow-fly in the blastula stage, showing the polar cells.

FIGS. 3 to 6.—Four sections of the ovum of the Blow-fly in the stage represented by Fig. 38.

The position of these sections is indicated by dotted lines in Fig. 38.

FIG. 3 represents a section taken in the region indicated by line 1.

FIG. 4 represents a section in the region indicated by line 2.

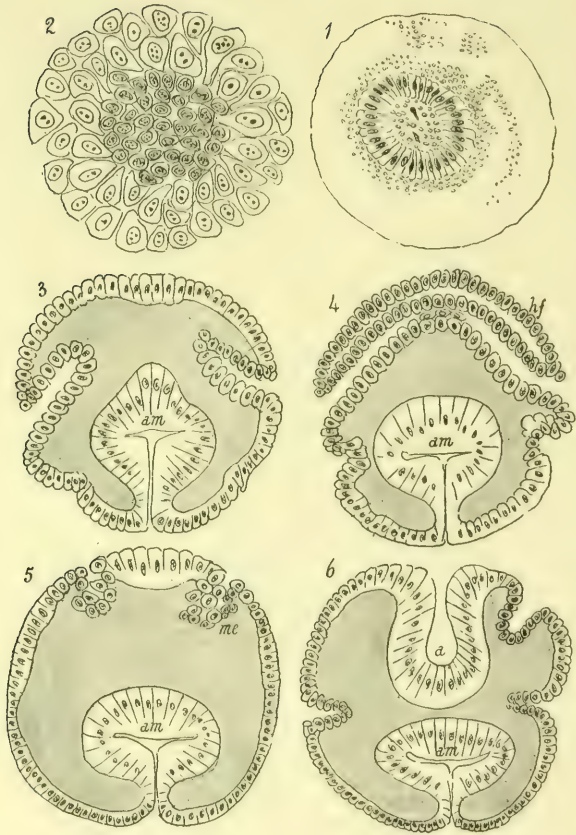
FIG. 5 represents a section immediately behind the head-fold, *hf'*.

FIG. 6 represents a section in the region indicated by line 3.

The following refer to all the figures in which they occur:

*a*, archenteron; *am*, amnion; *hf*, head-fold; and *me*, coelomic sac.

PLATE XIII.





In the fly-embryo the existence of an amnion and serosa has been denied. I have already figured (Fig. 2) what I believe to be the amnion and serosa when the embryo is in an early stage of development, but a short time later both apparently disappear.

At a still earlier period, before the primitive band is developed, ventral and lateral involutions of the blastoderm occur. These have been recently described by Graber [114] as ptychoblastic invaginations; I have given copies (Pl. XIII.) of several of his figures of transverse sections of an embryo, exhibiting a stage of extreme interest, which is also described and figured by Voeltzkow [111]. I am at a loss, however, to understand on what grounds Graber supposes these invaginations to be mesoblastic. I shall hereafter show that the mesoblast, as distinct from the parablast, has an altogether different origin. It appears to me that Graber's ventral ptychoblast, which Voeltzkow recognised to be the rudimentary condition of the whole primitive band, is the amnion, and Graber's lateral ptychoblasts are folds of the serosa. With regard to his dorsal ptychoblast, I regard it as the hypoblast undergoing invagination and converting the blastula into a gastrula.

I shall return to the subject of the dorsal ptychoblast of Graber, and in this place I shall deal exclusively with the ventral and lateral folds.

The ventral fold, which I consider the true amnion, is a thick-walled tube consisting of a single layer of large cylindrical epithelial cells, formed by a longitudinal invagination of the blastoderm, which is eventually closed by the coalescence of its ventral lips.

A comparison of this tubular thick-walled amnion with that of the embryo in the Aphides, as described by Will [108], shows that it closely resembles it. The pre-formation of a thick neural amnion in certain Rodents before the appearance of the primitive streak and neural groove is a precisely parallel phenomenon in Vertebrates.

It is very desirable to obtain more observations on the

changes which occur between the series of sections represented by Graber, some of which I have copied in Pl. XIII., and his series (Figs. 93 to 112) in which the primitive band is already developed. My own observations do something to bridge over the interval (Pl. XIV., Fig. 1), but are far from complete. As the changes occur between the third and fourth hour, according to Graber, they must be very rapid; and as, in my experience, the rate at which development in the egg progresses is determined by temperature, it is by no means easy to obtain sections in the exact stage needed for the observation.

In Fig. 38, 1, I have represented an ovum removed from the shell about four hours after impregnation. Until I saw Graber's figures I was at a loss to interpret the appearances exhibited, but by the construction given beneath it (Fig. 38, 2) this is no longer difficult. The great fold of the serosa, *h f, h f'*, is perhaps the 'Faltenblatt' of Weismann [2], about which so much uncertainty exists. I have never, however, seen it extending so far back as Weismann represents the 'Faltenblatt'; neither is it developed, as Weismann believed, from a head and tail fold. It is subsequently obliterated by the shortening of the primitive band.

The diagrammatic construction (Fig. 38, 2) exhibits a suggestive similarity to a Lamellibranch, or an Ascidian, which will be obvious to the morphologist. The great head-fold of the serosa resembles a mantle, and the amniotic tube is suggestive of the post-branchial chamber and atrium. The future position of the ventral cord and dorsal vessel of the insect both correspond with those of the nervous system and heart of the Lamellibranch. Moreover, it will be remembered that, whilst the greater part of the cellular wall of the blastocele only forms temporary structures in the Echinoderm and the Insect, the whole becomes part of the body of the Lamellibranch, just as the whole forms part of the insect embryo in the stage represented by my diagram. As I have no facts to guide me, except the similarity of the form and disposition of the parts, I am unable to pursue this subject further, and must leave the

consideration of the probability of any possible morphological connection between the embryonic form of the Insect and the Lamellibranch or Ascidian to be discussed by those who have made a special study of the Mollusca.

**The Primitive Band** (*Keimstreif*) may be described as a thickened band which usually appears on the ventral surface of the blastula. In the Lepidoptera a discoid thickening of the epiblast first appears, the germinal area, which, according to Graber [115], afterwards becomes a strap-shaped primitive band, wider at its anterior end. This change occurs as it sinks into the yelk. In many insects the primitive band occupies only a small portion of the ventral surface of the blastula; in others it extends over the whole ventral surface, and in some Diptera, as in the Muscidæ and Chironomus, at one period it surrounds the yelk; its anterior and posterior ends, if we include the large procephalic lobes, almost meeting on the dorsal surface of the yelk. The width of the primitive band is also subject to considerable variation. The lateral edges of the dorsal and ventral portions in the Blow-fly are only separated by a narrow chink, through which the food-yelk is seen as a dark line.

It is usual to designate the primitive band in Insects as endolecithal when it sinks into the yelk, as in the Lepidoptera, and epilecithal when it remains upon its surface, as in the Coleoptera. In many insects it is partly endolecithal and partly epilecithal. Whether the primitive band is endo- or epilecithal, the membranes have the same relation to the yelk, only in the latter case the serosa and amnion are so closely applied to each other that the yelk does not enter the inter-annial cavity (see Pl. XII.).

The origin of the primitive band in the Fly-embryo, according to the view I have adopted, is somewhat different, and closely resembles the manner in which the primitive band is formed according to Will [108], in the Aphides. It is developed from the cells which form the thick-walled amnial tube, only a few of which become flattened out to form the amnion. The cells of the primitive band are far smaller than those

which form the amnial tube, and evidently result from their subsequent division, whilst the greater part of the external layer of the blastoderm becomes converted into the serosa. Graber gives a figure of the primitive band and membranes in *Hylotoma*, one of the Saw-flies, in which precisely the same relations exist [115, Fig. 131].

**Structure and Segmentation of the Primitive Band.**—The primitive band has not been investigated at an early period of development in the Blow-fly embryo, so that I am only able to describe its structure from observations on other insects. It consists of a thickening of the epiblast, the result of a proliferation of its cells, but there is also a large development of parablastic elements, which penetrate between the deeper epithelial layers and form a sub-epiblastic stratum. These parablastic elements have hitherto been confounded with the mesoblast (Pl. XII., Fig. 7).

The primitive median furrow and the stomodæal pit appear at a very early period of development, and immediately afterwards the parablastic cells, which previously were evenly distributed on either side of the median furrow, break up into groups corresponding with the body segments. The cause of this separation of the parablast into groups of cells appears to me to be the rapid proliferation of the epiblast at the points where the nerve-ganglia are subsequently developed (Pl. XII., Fig. 6).

The process of segmentation has not been observed in the Blow-fly, or, indeed, in any of the Muscidæ at this early period. It evidently occurs with great rapidity, but there is no reason to suppose that it differs from that of other insects in which the numerous observations by various observers are all susceptible of the interpretation given above. The external layer of epithelium derived from the proliferating epiblast forms the hypodermis; the deeper cells develop into the primitive ganglia. The connective tissue and supporting investment of the ganglia, with the tracheæ, fat bodies and blood, originate from the parablastic layer.

**Contraction of the Primitive Band.**—During the segmentation

of the primitive band it gradually becomes shortened, and by the time this is complete the dorsal part of its epiblast is drawn back on the dorsal surface of the yelk and terminates at its posterior extremity, whilst the preoral lobes increase until they cover the anterior third of the yelk on its dorsal as well as its ventral aspect.

### 3. ORIGIN OF THE ARCHENTERON, SOMATOPLEURE AND CÆLOMIC SACS.

**Origin of the Hypoblast.**—According to most embryologists the archenteron in all the Metazoa originates by gastrulation, yet if the accepted origin of the hypoblast in Insects be correct, it appears to me it must be admitted that they conform in no way with the rest of the animal kingdom, but possess an alimentary canal developed in a manner which cannot be regarded as gastrulation.

I have already referred to two so-called gastrula stages (p. 240), but neither one nor the other can be said to be a modification of a typical gastrula. As the gastrula of *Amphioxus* or of an Echinoderm is regarded as typical, it is apparent that a true hypoblast must originate from the external covering of the blastocele, and may be said to be a mere invagination of the epiblast, or rather of the undifferentiated blastoderm, which becomes both epi- and hypoblast.

It is admitted that the process of gastrulation is much modified by the presence of a large food-yelk. In those Vertebrates in which such a yelk is present the epiblast is supposed to overgrow the hypoblast; but the true hypoblast is still a portion of the discoid blastoderm. According to Selenka, the primitive rudiment of the vertebrate archenteron is always an invagination of the primitive blastoderm, although, except in some fishes (Teleostei), it is no longer hollow beyond the anterior extremity of the primitive streak, which Selenka regards as the homologue of the posterior part of the alimentary canal.

The accepted view that the mesenteron in Insects is developed from cells which are formed in the yelk beneath the blastoderm,

appears to amount to this—that the archenteron is entirely parablastic; and such an hypothesis is without doubt completely at variance with all that is known of the development of the Metazoa generally.

The view which I adopt is that the so-called proctodæum in Insects is really a gastrulation, and is the true archenteron.

I was first led to this opinion by the relation of the cœlomic sacs with the so-called proctodæal opening, which I regard as a true blastopore; and I shall show that a great number of facts are in accord with my hypothesis, which is still further confirmed by the discovery of what I take to be a true proctodæal involution of the epiblast, near the posterior extremity of the ventral surface of the blastula (Fig. 3, p. 8).

It has long been known that in *Chironomus* the polar cells of Weismann travel forwards along the dorsal wall of the ovum during the formation of the primitive band, and then sink into the yelk. Balbiani supposed that these cells form the sexual glands,\* an opinion which has received much support.

In the Fly embryo the polar cells, by continued division, form a disc of small cells at the posterior pole of the ovum—my hypoblast—upon which a few spherical cells are sometimes seen to be adherent to the blastoderm. These, like the polar cells in *Chironomus*, travel forwards on the dorsum of the yelk, and sink into my archenteron at the dorsal extremity of the primitive band. Voletzkow has found them in the interior of the so-called proctodæal involution [111].

The involution of the blastoderm in the dorsal region of the embryo is preceded by the formation of a group of large cells at the spot previously occupied by the polar cells (Pl. XIII., Figs. 5 and 6). These form my primitive archenteron, and I term the orifice of invagination the blastopore. As the primitive band becomes shortened, the blastoderm between its hinder end and the blastopore assumes the same characters as the archenteric invagination (Fig. 38, p. 2). The edges of this part of the blastoderm become curved upwards, so that a groove is de-

\* Balbiani, E. G., 'Contribution à l'étude de la formation des organes sexuels chez les insectes,' Recueil. Zool. Suisse, Bd. ii., 1885.

veloped, which ultimately closes above and forms the metenteron. The metenteron then sinks into the yelk, and its blind posterior extremity, as I believe, eventually unites with the ventral proctodæal involution; but on this point I have no actual evidence, as I have been unable to trace the union of the hind gut and proctodæum, although it is clear that if I am right in the interpretation of the observations of myself and others, such a union must occur.

The mid-gut, that is, the part of the intestine in front of the blastopore, first turns backwards beneath the metenteron (Fig. 3), but its hinder blind extremity afterwards turns forwards

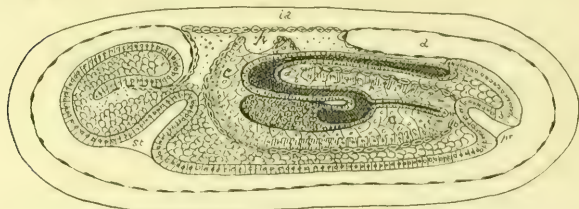


FIG. 39.—An ideal section of an embryo constructed from transverse sections, showing the relations of the archenteron, stomodæum, proctodæum, and cœlomic sacs. The parablatt of the cœlomic sacs and pericardial (segmentation) cavity, is represented by a chain of cells: *a*, amnial sac; *c*, cœlomic sac of the right side; *ia*, space between the amnion and serosa; *p*, pericardial cavity; *pr*, proctodæum; *st*, stomodæum.

and forms a solid cellular growth, which penetrates the yelk and ultimately becomes the mid-gut (Fig. 39).

The Malpighian tubes are developed as sacculi of the archenteron, one on either side of the blastopore, but subsequently travel back as far as the posterior extremity of the archenteric invagination, so that they open into it immediately behind its solid cellular portion.

If we compare the development of the archenteron of the fly embryo, as I have described it above, with that of the crayfish, as described by Huxley,\* it will be seen that a close correspon-

\* Huxley, T. H., 'The Crayfish: an Introduction to the Study of Zoology, Internat. Sc. Ser., vol. xxviii., London, Paris and Berlin, 1880.

dence exists between the two. According to Huxley, the archenteron in the crayfish is produced by an invagination of the blastoderm close to the posterior extremity of the embryo, on the dorsal surface of the yelk, and just in front of the proctodæal invagination, which Huxley terms the hind-gut.

The relation of the mesenteron to the yelk is precisely similar in the crayfish and fly embryos, and Huxley gives the following account of the manner in which the mid-gut of the former is developed: 'The embryo-crayfish remains only for a short time in the gastrula stage. The blastopore soon closes up, and the archenteron takes the form of a sac flattened out between the epiblast and the food-yelk, with which its cells are in close contact. Indeed, as development proceeds, the cells of the hypoblast actually feed upon the substance of the food-yelk.' He also adds in a footnote: 'Whether, as some observers state, the hypoblast cells grow over and enclose the food-yelk or not is a question which may be left open. I have not been able to satisfy myself of this fact.'

My own impression with regard to the development of the mid-gut of the fly embryo is that the solid portion of the invaginated hypoblast feeds upon, but does not enclose, the food-yelk, but I am not able to state positively that such is the case. The material which fills the mid-gut at a later stage of development resembles the small granular cells which replace the yelk, granular mesamœboids, but whether these have been enclosed by the wall of the mid-gut, or have immigrated into it through its epithelial wall, or whether they are developed

#### DESCRIPTION OF PLATE XIV.

FIG. 1.—A transverse section of an embryo five or six hours old, showing the relations of the primitive band, archenteron, amnion, and serosa.

FIG. 2.—A transverse section of an embryo ten hours old, showing the cœlomic sacs and pericardial (segmentation) cavity. The amnion and serosa are not seen in the section from which the drawing was made; they have been restored by dotted lines.

*am*, amnion; *am'*, amnial cavity; *ar*, archenteron; *cs*, cœlomic sac; *nc*, neural cord imbedded in parablast; *p*, pericardial cavity; *pa*, parablastic roof of the pericardial cavity; *s*, serosa; *y*, yelk.

PLATE XIV.

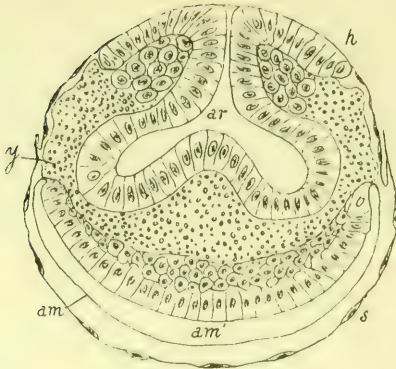


FIG. 1.

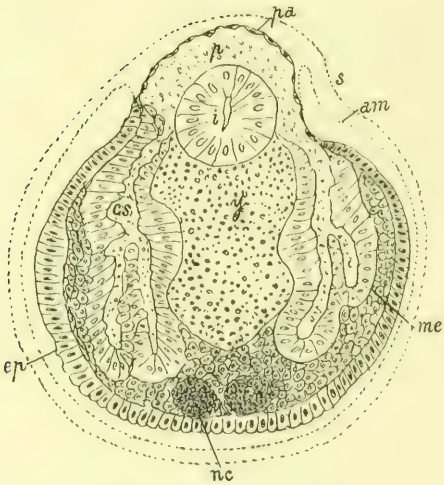


FIG. 2.



from the last polar cells which lie within the invaginated archenteron, is a matter which I cannot settle.

Will [108] describes and figures a group of cells in the aphid embryo, which he terms the sexual rudiment. It appears to me to be in reality the hypoblast, and to represent the polar cells of the Diptera.

**Formation of the Somatopleural Epiblast.**—During the development of the archenteron the epiblast of the primitive band extends laterally and grows upwards over the yelk, separated from it by the thick layer of parablastic cells, in which the rudimentary ganglia of the ventral chain are imbedded (Pl. XIV., Fig. 2), so that the embryo becomes boat-shaped (Fig. 40).



FIG. 40.—An embryo of the Blow-fly removed from the egg before the somatopleural epiblast closes over the dorsal surface of the yelk.

It will be seen by the figure that before the segmentation of the body is apparent externally, the great procephalic lobes meet upon the dorsal surface of the head, and the fore-head appears as a vesicle on its ventral surface, in front of the stomodæum. The rudiments of the mandibles and maxillæ are also present as thick folds on either side of the primitive mouth. At this stage the dorsal surface of the yelk is only covered by parablast, which bounds a cavity, regarded by Chodkowski as representing a segmentation cavity.

**Origin of the Mesoblast.**—At a very early period of development a pair of involutions occur, one on either side of the primitive hypoblast (Pl. XIII., Fig. 5, and Pl. XIV., Fig. 2). These I regard as the cœlomic sacs. They afterwards become

very large, and extend on either side of the yelk to the anterior and posterior extremities of the embryo. They then lose their connection with the alimentary canal, but remain open in front of the intestinal flexure corresponding with the original blastopore, and communicate with the segmentation cavity of Cholodkowsky. This cavity (*p*, Fig. 39) is produced by the contraction of the primitive band, and it communicates with the yelk in front of the cœlomic sacs and behind the procephalic lobes. As the primitive band contracts, the head and tail-folds of the amnion separate, so that the cavity, *p*, is only divided from the inter-amnial space by its roof of parablast. It becomes the pericardial cavity.

**Segmentation of the Somatopleure and Cœlomic Sac.**—Even before the epiblast of the somatopleure covers the dorsal

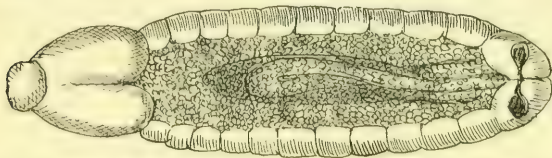


FIG. 41.—A dorsal view of an embryo before the somatopleural plates meet on the dorsum of the yelk, showing their segmentation.

surface of the yelk, the annular segmentation of the larva becomes apparent by the formation of deep inflections between the segments. These inflections at first only involve the epiblast, but soon extend to the mesoblast.

The cœlomic sacs form two cellular plates, with a third incomplete plate between them (Pl. XIV., Fig. 2). The external and internal plates become adherent to the involutions of the epiblast between the somites, so that each cœlomic sac is divided into a series of secondary cavities, corresponding in number to the annuli of the epiblast.

I have not hitherto seen this stage of development in any of my sections, but Graber gives figures of embryos in which each somite exhibits a distinct cavity between the outer and inner cœlomic plates.

The cœlomic plates ultimately form the somatic muscles, and I am inclined to think that the inner plate (the Darmdrüsenblatt of the Germans) enters into the formation of the muscles of the alimentary canal.

**Cholodkowsky**<sup>\*</sup> has very carefully studied the development of the cœlomic cavity in '*Blatta Germanica*,' and arrives at the following conclusions, which are quite consonant with the view I have given above of the changes which the cœlomic sacs undergo in the Blow-fly embryo :

1. 'In "*Blatta Germanica*" the body cavity is developed from eighteen pairs of hollow somites, which originate from the segmentation of the epiblast and cœlomic sacs.'

2. 'The cavities of the somites each divide, as in *Peripatus*, into three parts, one of which is probably homologous with the segmental funnel.'

3. 'The somatic cavities ultimately become broken up (*aufgegeben*), and open into the pericœlomic space, which corresponds with the segmentation cavity, and is permeated by the parablast.'

4. 'The cœlom, or body cavity, in its definitive stage, has therefore a three-fold origin ; it consists of the primitive cavities of the somites (*i.e.*, the cavities of the segmented cœlomic sacs), of the primitive segmentation cavity, and of a true schizocœle, which is subsequently formed.'

I am unable to trace any appearance of a true schizocœle in the Fly embryo, but think it probable that only a small portion of the inner cœlomic plate enters into the formation of the alimentary canal. If this is so, a schizocœle may be assumed to exist, although the invasion of its cavity by spongy parablast masks its true character.

5. 'The heart is developed from the primitive segmentation cavity.' I think this statement should be: the segmentation cavity forms the pericardium, not the heart.

6. 'The fat bodies are derived from yelk cells, which at a certain stage are amœboid, and wander into the body cavity.' This is merely another form of the statement that the fat bodies are of parablasic origin.

7. With regard to the origin of the cœlomic sacs in *Blatta*, the memoir quoted gives little information, but at the moment of going to press I received a much-extended memoir of Cholodkowsky's on the development of *Blatta Germanica*.† In this paper he states that the mesoblast (his inner germinal layer) is derived from an invagination which takes place in the ventral median line, the primitive trace (*Primitivrinne*). I think that the drawings given by Cholodkowsky of the primitive trace, which are accurate representations of sections, do not bear the interpretation he puts upon them. In this I am in unison with Tichomirow, who denies that the primitive trace has anything to do with the formation of the mesoblast.

\* Cholodkowsky, N., '*Zur Embryologie von Blatta Germanica*,' Zool. Anzeig., Bd. xiii., p. 137, 1890.

† Cholodkowsky, '*Die Embryonalentwicklung von Phyllodromia (Blatta) Germanica*,' Mem. de l'Acad. Imp. des Sc. de St. Petersburg, tom. xxxviii. No. 5, 1891.

In this connection I would mention that Metschnikoff\* figures coelomic sacs in *Simulia* exactly similar to those I claim to have discovered in the Fly embryo, although they are unlettered in his figures, and are not referred to in his text. As Metschnikoff only saw them in optical section, he apparently mistook them for the remains of the yelk. Similar appearances are also seen in the embryo of *Chironomus*.

#### 4. THE DORSAL ORGAN OF KOWALEVSKI.

Kowalevski [97] first described a structure in *Hydrophilus* which he termed the dorsal organ. He regarded it as a thickening of the outer provisional membrane, the serosa, and states that it afterwards forms a tube and sinks into the yelk. Graber† has more recently investigated the subject, and accords with Kowalevski; but both Graber and Kowalevski regard the whole of the blastoderm beyond the primitive band as serosa. In Lina, Graber derives the dorsal organ from the amnion, and Cholodkowsky states that it is formed from the serosa in *Blatta*.‡

It appears to me that these differences arise partly from a confusion of nomenclature, and partly from the very extraordinary changes of position which the amnion is believed to undergo by Graber. The dorsal plate always originates from a portion of the blastocele which is in contact with the yelk.

Cholodkowsky says that its development in *Blatta Germanica* is well seen, and that the dorsal margin of the posterior amnial fold ends in a thick plate of contracted serosa, consisting of tolerably high cylindrical cells, the dorsal organ. This plate becomes shortened, and forms an oval fossa, which is invaginated in the food-yelk. From the bottom of the invagination large, irregular, often amœboid, cells arise and wander into the yelk.

Cholodkowsky's figures convince me that his dorsal organ is my mesenteron. The scattering of the cells in the yelk, which

\* Metschnikoff, E., 'Embryologische Studien an Insecten,' Zeitsch. f. w. Zool., Bd. xvi., 1866.

† Graber, V., 'Vergleichende Studien über die Keimhüllen und die Rückenbildung der Insecten,' Denkschrift. K. Akad. Math. Naturwiss. Cl. Wien, Bd. lv., 1888.

‡ Mem. de l'Acad. St. Petersburg, tom. xxxviii.

he believes occurs, is, I think, the result of imperfect fixation; and I have no faith in the method employed by Cholodkowsky (chromo-nitric acid).

Graber gives beautiful figures of the dorsal organ in *Hydrophilus*, *Melolontha*, *Pyrrhocoris*, and *Musca*, although in the latter he mistook it for a ventral invagination. In all these insects it becomes an epithelial tube.

Graber, after describing the formation of the dorsal tube by the invagination of the dorsal plate (his dorsal ptychoblast) and its sinking into the yelk, says: 'The cells give off amœboid processes, which probably feed upon the yelk.' At a later stage, according to Graber, it separates into its constituent cells, which become wander-cells in the yelk. In these statements Graber and Cholodkowsky agree so far as *Hydrophilus* and *Blatta* are concerned; but Graber has more recently described the same organ in the Blow-fly embryo as the rudiment of the hind gut.

The identity of Graber's hind gut in the fly embryo with Kowalevski's dorsal organ and with my archenteron is certain. The only questions which remain uncertain are: Are Graber and myself right in maintaining that it is part of the alimentary canal in the Muscidæ? And is Graber right in regarding it as the hind gut, or am I right in regarding it as a typical gastrulation forming the archenteron?

I hold that the dorsal plate, when it first appears in the fly embryo, is neither covered by the amnion nor serosa, and that these membranes extend over it subsequently. Compare Graber's diagram (*l.c.*, p. 254; Fig. 20, p. 18), which shows the membranous fold of the amnion and serosa overlapping it in *Hydrophilus*. Of course, if the whole blastoderm outside the primitive band is called serosa, and not only its folds (*Faltenblätter*), then the dorsal plate is developed from the serosa.

Graber, in *Lina*, derives it from the amnion, which he thinks first splits in the ventral median line, then travels through the yelk to the dorsum, where its torn edges reunite. This theory appears to me so improbable that I cannot entertain it.

The idea that the membranes, amnion and serosa, undergo

rupture during development is very old. Weismann conceived that in most Insects the development of the primitive band is accompanied by a rupture of the blastodermic vesicle. He divided Insects into two groups, one in which he believed such splitting occurs, which he named *regmagene Insecten*; others in which he believed no rupture to occur he styled *aremagene*.

According to the same authority, Chironomus, Simulia, Pulex, Donacia, and Phryganea are 'regmagene,' whilst Musca and Melophagus are 'aremagene.'

E. Metschnikoff,<sup>\*</sup> in 1886, said on this point: 'Although it must be admitted that the primitive band has not the same relation to the remainder of the blastoderm in different insects, it must not be concluded that it is differently developed since no tearing of the blastoderm occurs. The variation is due to the complete or incomplete character of the amnion.'

In Weismann's 'aremagener Insecten' no amnion is developed, and, as I have already stated, an amnion is developed in the fly embryo. If I am correct in this, unless the Pupiparæ are without an amnion, Weismann's second class, regarded as insects in which the amnion is not formed, does not exist.

According to my observations, the development of the fly embryo is very similar to that of Chironomus, as given by Weismann, and the apparent rupture of the serosa described by him in the latter is merely the result of the shortening of the primitive band and the separation of the head and tail folds.

I confess that the exact relation of the dorsal plate to the amnion has greatly puzzled me, although, if Graber's figures are correct (Pl. XIII.), it is clearly first formed before the serosa exists, and, if my interpretation of them is right, when the amnion is a thick-walled epithelial tube; and is only afterwards covered by the extension of the amnion and serosa over the dorsal surface of the embryo.

It is important to remark that both the dorsal involution of

<sup>\*</sup> *L.c.*, p. 254.

the dorsal plate and the proctodæum exist at the same time in *Hydrophilus* (Graber) and in *Blatta* (Cholodkowsky), as this is strong confirmatory evidence in favour of my statement that the proctodæum and dorsal involution are distinct in the fly embryo. Moreover, it disposes of Graber's contention that the dorsal invagination—my archenteron—is a hind gut, and it establishes the relation of the Malpighian tubules with the mid-gut, and not with the proctodæum (see Development of Malpighian Tubules).

#### 5. THE NYMPHOID STAGE OF THE EMBRYO AND ITS CONVERSION INTO THE LARVA.

**The Nymphoid Stage of the Embryo.**—About twelve hours after impregnation the embryo has assumed what I term the nym-



FIG. 42.—An embryo about twelve hours old in the nymphoid stage. (After Weismann.)

phoid stage; the procephalic lobes meet in the middle line above, and the rudiments of the cephalic post-oral appendages attain their maximum development. The head-capsule in front of the mouth and between and below the procephalic lobes projects as a vesicular swelling—the fore-head. The remainder of the embryo is segmented as in the larva. In this condition it has a closer resemblance to the nymph than at any intermediate period; the thoracic appendages are, however, entirely wanting, and the rudimentary cephalic appendages exhibit a very generalized type.

**Formation of the Larva.**—After the twelfth hour the retrogression of the developmental process becomes apparent, and



PLATE XV.

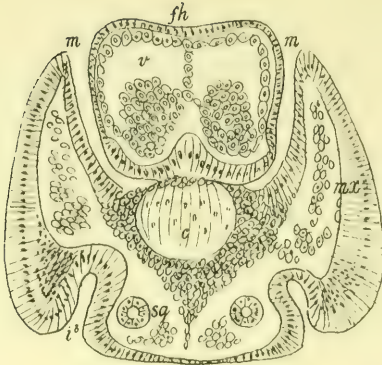


FIG. 1.



FIG. 2.

EMBRYO, LATE STAGE.



unite behind the mouth and rapidly undergo a great reduction in size; they form the labium.

There is no doubt in my mind with regard to the fate of the procephalic lobes and fore-head, although the meagre facts which have been hitherto recorded are by no means in perfect accord with my view. Weismann is the only author who claims to have observed the phenomena, and his observations are somewhat vague, and in some points, I think, incorrect.

The changes which take place during the involution of the procephalic lobes will be more readily understood by a reference to Figure 44 than by the most lengthy description. They are probably brought about by the rapid growth of the anterior part of the stomodæum; and by the increased size of the somites developed from the somatopleure, which causes the prothoracic segment to advance towards the anterior extremity of the embryo.

I have sections which show that the procephalic lobes form a double involution on each side, and, from the condition of the great cephalic discs in the newly-hatched larva, I think it is manifest that their antennal and optic rudiments are formed by the invagination of the procephalic lobes. Although I have not been able to demonstrate the invagination of the fore-head at this period, it undoubtedly rapidly disappears, and the invagination of this part is so clearly seen in the newly-hatched larva, that I can see no reason to doubt that it forms the cavity above the labrum already described (p. 41). This communicates below with the sacs which enclose the antennal and optic rudiments or discs.

Weismann says: 'When the fore-head is definitely separated from the procephalic lobes, it appears as an obliquely truncated process, having the form of a four-sided prism. Its ventral surface is convex, but neither this nor the upper flat surface exhibits any median fissure. After the anterior maxillæ become parallel, the fore-head is bent towards the abdominal surface, and rapidly assumes a position in which its anterior truncated surface becomes ventral; its ventral surface covers the mouth and lies upon the primitive band, which is only separated from

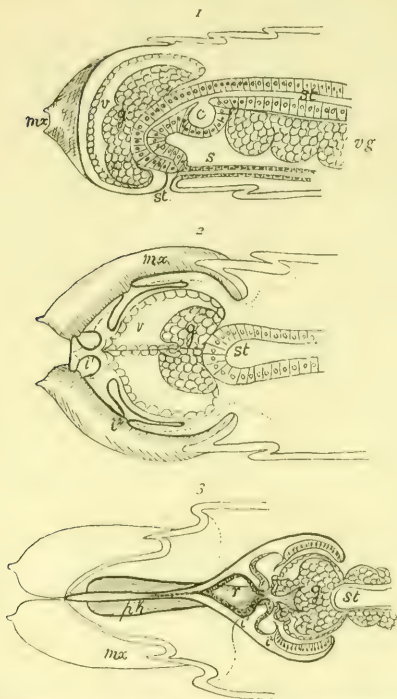


FIG. 44.—Three diagrams representing the manner in which the head discs and nervous system of the embryo are related—1 and 2, before the retraction, and 3, after the retraction, of the fore-head to form the cephalo-pharyngeal sac: *c*, the crop; *g*, cephalic ganglion; *i*<sup>1</sup>, antennal, and *i*<sup>2</sup>, optic discs; *mx*, first pair of maxillæ; *ph*, cephalo-pharynx; *r*, the ring; *s*, salivary duct; *st*, stomodæum; *v*, hollow ventricle of the brain; *vg*, ventral ganglia. The invaginated epiblast in 3 is represented by a dark single line in 1 and 2. The dotted lines in 2 and 3 trace the course of the tracheal vessels of the discs, which arise close to the position of the future anterior spiracle. 1 and 2 represent embryos in the stage from which the sections represented in Plate XV. were taken; 3 exhibits the relations of the parts in the young larva.

it by a transverse line. The mandibles at this period lie in the mouth-cleft, and sink more and more deeply into it. It is remarkable that the fore-head takes no part in the formation of the larval head, but is entirely invaginated' [2, p. 64].

On this point Weismann adds: 'After the invagination of the fore-head within the mouth, both pairs of maxillæ grow forwards; especially the anterior, which become considerably enlarged, project beyond the fore-head, and draw the procephalic lobes together, whilst the latter become smaller and smaller, and unite with the maxillæ [2, p. 67].

With the exception of the last statement, Weismann's account appears to me to be quite correct. Weismann believed that the dorsal sensory organs on the maxillæ of the larva represent antennæ, and hence he supposed that the procephalic lobes unite with the rudimentary maxillæ.

Van Rees [147] confirms by his views and observations an opinion which I expressed as early as 1872 [142], that the procephalic lobes are invaginated to form the cephalic discs, although Graber is led to a different conclusion, as he asserts that these discs in the fly embryo are at first composed of a single layer of cells [114]. Certainly, his drawings lead to such a conclusion, but in the face of the evidence afforded by my sections and the observations of Van Rees, I cannot regard Graber's sections as conclusive. It is possible that certain sections, through the thick edges of the discs, would present these appearances, but I think it probable that further investigations will show that the disc cavity which exists at the earliest stage of development is never entirely obliterated. Graber's sections are apparently made from embryos in a more advanced condition than mine, and it may be that at this stage the disc cavity is relatively small, and that the edges of the disc form considerable solid outgrowths, over which the cavity subsequently extends; but on this point further observations are needed. In newly-hatched larvæ the disc cavities are certainly distinct.

## CHAPTER VIII.

### THE GENERAL ANATOMY OR HISTOLOGY OF THE BLOW-FLY.

It will perhaps be useful to the general reader, as well as to the student, who may not be conversant with the peculiarities of the tissues in insects, to devote a chapter to their consideration, before entering upon a description of the developmental

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**Bibliography.**—As recent histological literature is very extensive, the reader who wishes for an extended Bibliography is referred to Quain's 'Anatomy,' 10th edit., 1891, vol. i., part 2, 'General Anatomy or Histology.' The following works are more or less especially devoted to the histology of Insects, or are quoted in the text :

122. LEYDIG, F., 'Zum feineren Bau der Arthropoden.' Müll. Archiv., 1855.
123. LEYDIG, F., 'Lehrbuch der Histologie des Menschen und der Thiere.' Frankfurt-a-M., 1857.
124. WEISMANN, A., 'Ueber die Zwei Typen contractilen Gewebes und ihre Vertheilung in die grossen Gruppen des Thierreichs, sowie über die histologische Bedeutung ihrer Formelemente.' Zeitsch. f. ration. Medicin, Bd. xv., 1862.
125. LANDOIS, H., 'Beobachtungen über das Blut der Insecten.' Zeitsch. f. w. Zool., Bd. xiv., 1864.
126. BÜTSCHLI, O., 'Zur Entwicklungsgeschichte der Biene.' Zeitsch. f. w. Zool., Bd. xx., 1870.
127. BALBIANI, E. G., 'Sur la structure du Noyau des cellules salivaires chez les larves de Chironomus.' Zool. Anzeiger, 1880, p. 662.
127. VIALLANES (see page 25). Ann. Sc. Nat., ser. vi., T. xiv.
128. LEYDIG, F., Zelle und Gewebe. Neue Beiträge zur Histologie des Thierkörpers, 8vo, Bonn, 1885.
129. CARNOY, J. B., 'La Cytodière chez les Arthropodes.' La Cellule, T. iii., Louvain, 1886.
130. FRENZEL, J., 'Einiges über den Mitteldarm der Insecten sowie über Epithelregeneration.' Archiv f. mikros. Anat., Bd. xxvi., 1886.
131. SHÄFFER, C., 'Beiträge zur Histologie der Insecten.' Spengel. Zool. Jahrbuch, Bd. iii., 1887.
132. FAUSSEK, V., 'Beiträge zur Histologie des Darmkanals der Insecten.' Zeitsch. f. w. Zool., Bd. xlix., 1887.

changes which occur in the pupa, and before giving a detailed account of the various organs of the imago.

Upon making a careful examination by the aid of the microscope, it will be found that the number of distinct forms of texture or tissue is comparatively small, and, although many differences may be observed in different parts, a study of the transitional forms shows that all the tissues may be classed under one or other of the following heads:

1. Epithelial tissues.
2. Amœboid cells.
3. Connective tissues.
4. Muscular tissues.
5. Nervous tissues.

When any tissue is examined with the microscope, it may be resolved into a number of parts, which are repeated over and over again. These parts are termed tissue-elements, and many tissues retain certain structural elements which are termed cells, and which closely resemble the primary cell from which the whole body is developed. Others, as the muscles and nerves, although developed from cells, soon become so modified that their cellular character is not apparent at first sight, but a careful study shows indications of their cellular origin.

In addition to the cellular constituents, many of the tissues exhibit a more or less homogeneous intercellular substance,

133. RATH, OTTO VON, 'Hautsinnes-organe der Insecten.' *Zeitsch. f. w. Zool.*, Bd. xlv., 1888.
134. BÜTSCHLI UND SCHEWIAKOFF, 'Ueber der feineren Bau der quergestrihten Muskeln der Arthropoden.' *Biol. Centralblatt*, Bd. xi., p. 33, 1891.
135. SCHÄFER, E. A., 'On the Minute Structure of the Muscle-Columns, or Sarcostyles, which form the Wing-Muscles of Insects.' *Proc. Roy. Soc. Lond.*, vol. xlix., p. 280, 1891.
136. SCHÄFER, E. A., 'General Anatomy or Histology.' Quain's 'Anatomy,' edit. x., vol. i., pt. 2., published separately. London and New York, 1891.

termed the matrix. This matrix may be laminated, and the cuticle of insects has been regarded by some as substantially an intercellular matrix. Other matrices exhibit a distinct fibrillation, as in fibro-cartilage, but I am in doubt if such are ever found in insects, although fibrillation of the cuticular layer has been described in Crustacea and Arachnids.

The various tissues may be arranged according to their origin. Thus the epithelial, nervous and muscular tissues are developed from the cells of the blastoderm, whilst the amœboid cells and the connective tissues originate from the parablaster.

The principal modifications exhibited by cells and nuclei may be conveniently considered first, and a description of the several tissues classified under the subjoined heads will follow :

1. The parablasteric tissues.
2. The epithelia; and
3. The muscles and nerves.

## 1. CELLS AND NUCLEI.

**Cells.**—The parts called cells are corpuscles, which are very similar in insects and in all other animals; indeed, they cannot be said to differ in any essential character from those of which the human body is built. In the fly the largest cells are  $\frac{1}{100}$  of an inch in diameter, or twice as large as the largest in the human body, whilst the smallest do not exceed  $\frac{1}{10000}$  of an inch, and are smaller than any of those found in the tissues of man. Some cells have a distinct outer wall, or cell-wall; all possess a main substance termed cell-substance, or protoplasm; and all have a central body imbedded in the protoplasm, termed the nucleus.

**The Cell Substance**, or protoplasm of a cell, consists of a fine reticulum, or network, radiating from the nucleus, termed *spongioplasm*, and of an apparently structureless substance, which occupies the meshes of the spongioplasm, known as *hyaloplasm* or *enchylema*.

An amœbiform or amœboid cell consists only of cell-substance enclosing a nucleus ; it possesses the property of spontaneous movement by means of pseudopodia, like an amœba, and is capable of ingesting solid and fluid materials, which appear as globules or granules in its interior.

Many mature cells have a large quantity of granular material, and others have oil, as, for example, the fat cells, stored in their protoplasm—Cell contents. Such stored material is usually formed by the cell, and is sometimes present in so large a quantity that the cell-substance forms a mere wall around the contents. It is from this form of cell, which was first discovered, that the appellation has been extended to all cells. It has therefore acquired a new and technical meaning.

Non-amœboid cells are usually called 'fixed,' and are frequently surrounded by a distinct film, or cell-wall, either secreted by or formed from the protoplasm of the cell. The cells in Insects are united either by the fusion of their protoplasm, when the spongioplasm of one cell may be traced into those adjacent to it, or by an intercellular cement material, and rarely by a more copious matrix.

**Mucoid Degeneration.**—The part of the protoplasm of a cell which is exposed, either by reason of the cell forming a portion of the surface of the body, or of the lining of the alimentary canal, is sometimes observed to become clear and transparent, and to stain very feebly or not at all. This part of the cell consists of mucin, or of that modification of mucin termed chitin. It is the result of a change in the character of the cell substance itself, and, as this material exhibits none of the vital properties characteristic of protoplasm, its formation may be regarded as a kind of degeneration.

The great cells of the fat bodies of Insects are surrounded by a thin pellicle of chitin, which forms the cell-wall.

Whether the mucin or chitin formed by cells is to be regarded as an excretion or as a modification of the cell substance has long been a matter of speculation. From the changes which occur in the cells of Insects, I have no hesitation in

regarding it as a direct modification of the cell substance, and not as an excretion formed in the cell and poured out on its surface. I shall hereafter recur to this point.

**The Nucleus.**—The appearances presented by nuclei are much more diverse than those exhibited by cells. The nucleus exists in two conditions—the resting stage, which is characteristic of a cell which is not undergoing division, and the active nucleus, in the dividing cell.

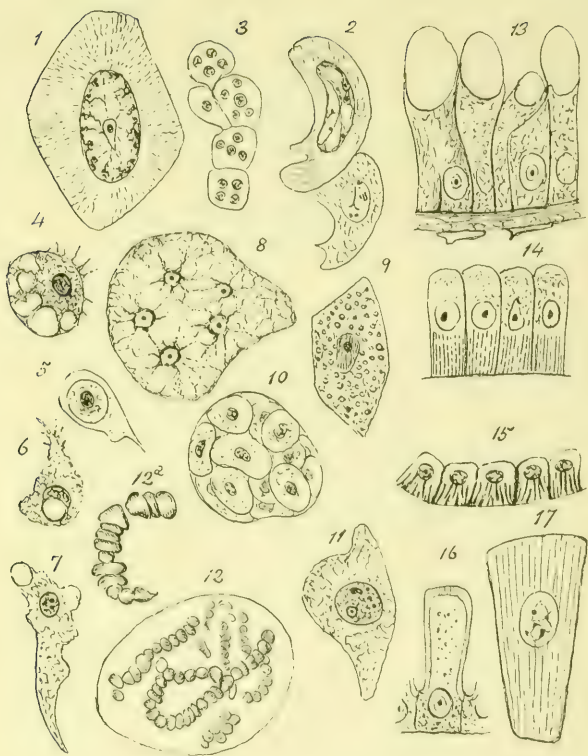
**The Resting Nucleus** in insects is generally enclosed in a thin capsule, and consists of a clear plasma, *nucleoplasm*, in which a reticulum, or long coil of fibre, is seen; this fibre is termed the nuclear fibre or nuclear skein. It consists of granules, *chromatin granules*—so called from their affinity for such dyes as logwood or carmine, *nuclear stains*, when properly applied (see Appendix to Chap. IV.). The chromatin granules are united by a substance which does not stain—*achromatin*.

#### DESCRIPTION OF PLATE XVI.

Cells and Nuclei, exhibiting their principal modifications.

- FIG. 1.—A large epithelial cell from the hypoderm of the larva, with striated cell substance, a vacuolated nucleus, and a nuclear nucleolus.  
 FIG. 2.—Two hypodermal cells from the larva in the resting stage.  
 FIG. 3.—Multinucleate pericardial cells from the young nymph, possibly young fat cells.  
 FIG. 4.—An amœboid cell from the blood of the young imago, loaded with droplets of oil.  
 FIG. 5.—An amœboid cell from the blood of the young imago.  
 FIG. 6.—An amœboid corpuscle from the same, enclosing a vacuolated nucleus.  
 FIG. 7.—A similar cell with a single droplet of oil in its interior.  
 FIG. 8.—The cell-capsule of an exhausted fat cell from an adult egg-laying female, showing stellate daughter cells.  
 FIG. 9.—A young fat cell from the imago.  
 FIG. 10.—The nucleus of a fat cell from the nymph filled with leucocytes.  
 FIG. 11.—An epithelial cell from the hypodermis of a larva, showing the intracellular reticular spongioplasm; the nucleus enclosing a nuclear nucleolus.  
 FIG. 12.—The nucleus of a salivary cell from the larva, showing the nuclear thread.  
 FIG. 12a.—A portion of the nuclear (chromatin) thread, showing the chromatin beads.  
 FIG. 13.—Goblet cells from the proximal intestine of the imago.  
 FIG. 14.—Secretory epithelial cells, from the proximal intestine of the imago.  
 FIG. 15.—Rodded salivary cells from the sericterial glands of the imago.  
 FIG. 16.—Epithelial cell from the distal intestine of the imago, with a striated border.  
 FIG. 17.—Large cell from the rectal papilla.

PLATE XVI.





In the resting nucleus the nuclear fibre is sometimes replaced by a reticulum, or even by scattered masses and granules of chromatin.

**Growth of the Cells of the Larva.**—During the larval stage the epithelial cells of the hypodermis and alimentary canal, as well as those of the salivary glands and fat bodies, do not undergo multiplication, cell-division ceasing with the hatching of the egg or soon after. The rapid growth of the larva results from the increase in the size of the cells, so that when full-grown these attain a magnitude which is quite exceptional. Those of the lingual (salivary) glands frequently measure  $150\mu$  to  $200\mu$  ( $\frac{1}{15}$  inch), and have nuclei from  $50\mu$  to  $60\mu$  in diameter.

**Nuclei of the Salivary Cells.**—The nuclei of these gigantic cells are very favourable objects for the study of the resting nucleus. If a larva is opened and immersed for half an hour in Flemming's mixture (see p. 94), and then washed for twenty-four hours in 75 per cent. alcohol, the salivary glands can be dissected out, and after staining with Erhlich's hæmatoxylin, the individual cells can be mounted in balsam in the usual way. Such a preparation exhibits the structure of nuclei admirably. Or the cells may be separated after a few minutes' immersion in Flemming's mixture and examined in it; under this treatment the nucleus in each cell exhibits a very delicate investing membrane. In some cases I have seen such a nucleus divested accidentally of all cell protoplasm as a distinct vesicular spheroid, and I have even observed the rupture of the investing membrane, and the escape of the contents—a clear, apparently fluid substance, in which the nuclear threads lie in a more or less dense tangle.

The nuclear thread consists of large bead-like chromatin granules, varying from  $2\mu$  to  $4\mu$  in diameter, flattened where they are in contact with each other, sometimes exhibiting the appearance of a series of cups and balls. The stained granules are invested by an unstained substance, which unites them with each other. Balbiani [126] described a similar condition in the nuclei of the salivary glands of *Chironomus*, and Viallanes [27, p. 169] states that Henneguy announced to him

that he had observed the same thing in *Musca*. Eimer\* has recorded the appearance of the non-stained thread uniting the chromatin granules.

Carnoy [129] describes the nuclear thread of insects as composed of numerous minute chromatin granules, united by a clear material, and states that they sometimes surround a central cavity, or, in exceptional cases, form a spiral fibre. I have never seen these appearances, and this is the more remarkable as Carnoy describes them as occurring in the hypodermis of the Blow-fly larva. My failure to do so is probably due to a different method of preparation. When fresh nuclei are examined in Flemming's mixture, or even in normal saline solution,† I have repeatedly seen the nuclear threads divided into transparent discs, which remind me of rouleaux of human blood corpuscles, except that they are smaller and colourless. They are highly refractive.

It is a fact worthy of note that, although the nuclear skein is so well developed in the large nuclei of the salivary cells, the fat bodies, and the epidermis, these cells never undergo division, and are destined to be completely destroyed by the action of phagocytes in the first days of the pupa stage (see Chap. IX.).

**Nucleoli.**—It frequently happens that one or two larger, highly-refractive masses are seen suspended in the nucleoplasm; these are termed nucleoli. Some regard them as mere isolated masses of chromatin; others, as distinct in nature and chemical composition.

I am inclined to think that the history of nucleoli has yet to be written. Some are undoubtedly merely the remains of a degenerated or degenerating nuclear thread. Such masses are sometimes comparatively large and irregular in form; they are seen in numbers in the degenerated tissues of the pronymph. Others, which are distinguished by Carnoy as nuclear nucleoli, resemble a minute nucleus, and have granules of chromatin in

\* Eimer, 'Ueber den Bau des Zellkerns,' *Archiv f. mik. Anat.*, Bd. xiv.

† A 0.65 solution of common salt.

their interior. Some nucleoli exhibit distinct amœboid movements; such appear to me to be young nuclear nucleoli. These nucleoli are possibly the nuclei of immigrant phagocytes, which have found their way into the large nuclei of degenerating cells: compare the nuclei of leucocytes (Fig. 17), which exhibit all the varieties of form ascribed by Carnoy to nuclear nucleoli. In some cases at least this explanation is undoubtedly correct.

**The Paranucleus** (*Nebenkern*).—It sometimes happens that a more or less shrivelled, irregular mass of material is found outside a nucleus. This mass stains readily, and has been termed the paranucleus; such paranuclei are occasionally seen in epithelial cells. The nature of the paranucleus is unknown, but, in some cases at least, I believe I have traced its origin to a degenerated nucleus. After division one nucleus remains, and the other undergoes degeneration. I shall hereafter recur to this subject.

**The Active Nucleus.**—Before and during the division of the nucleus, a phenomenon which always precedes the division of a cell, the nuclear fibre is seen to undergo remarkable changes in its arrangement. These changes are spoken of as karyomitosis, or karyokinesis. The student will find an account of them in any modern text-book on histology. When these changes occur, the division of the nucleus is said to be indirect.

The indirect process of nuclear division is of very wide, if not universal, occurrence in both animals and plants.

The old view was that a nucleus undergoes simple fission, a change which is termed the direct mode of nuclear division. Many observers have entirely denied its occurrence since the discovery of indirect division.

At one time I thought that the large nuclei of many insect tissues would afford favourable objects for the study of indirect cell-division, but, although the nuclear thread is well developed in them, they unfortunately do not divide. And I have been unable to observe indirect nuclear division in insects satisfactorily except in the early stages of spermatogenesis. Although

nuclear spindles have been described in the ova, and I have no doubt of their occurrence, I have not observed them in any of my preparations.

The cells of the embryo and of the imaginal discs are so small that they are not favourable objects for the observation of karyomitosis. Large multinuclear cells occur, however, in both the larva and imago in the form of cell-chaplets (see pp. 61 and 85), in which the nuclei are undoubtedly undergoing multiplication, and in these I have been quite unable to discover nuclear figures.

Nor, so far as I know, has anyone ever claimed to have observed the phenomena of karyomitosis in these cells. The direct division of the nucleus has been observed by me in the blood corpuscles, leucocytes, of the larva, but under circumstances unfavourable for the observance of karyomitosis if it occurs (see page 271); so that I regard the occurrence of direct division as an open question, but still hold that it is probable.

## 2. THE PARABLASTIC TISSUES.

The tissues or tissue elements traced to the parablast or mesenchyme (see page 235) are the blood corpuscles, the connective reticulum which forms the bed in which the tracheal capillaries lie, the fat bodies, the oinocytes, and the multinucleated cell-chaplets. Phagocytes are probably merely modified blood cells, but whether all phagocytes are derived from these, or indeed solely from the parablasic tissues, although probable, cannot be positively asserted.

**The Blood Corpuscles** are amœboid cells, measuring from 6 to 12 $\mu$  in diameter. They are far more abundant in the resting larva and pronymph than in the imago. In the larva they exhibit resting nuclei, with a single, highly refractive nucleolus and little chromatin. In this stage I have observed the direct division of the cells. The process occupies about half an hour. The nucleus is first withdrawn to one end of the cell (Fig. 17 *bis*, 3*a*), and a constriction then occurs in the equator of the cell. This

subsequently disappears and the nucleus returns to its central position. Such changes recur many times, the equatorial constriction of the cell being more marked with each repetition of the phenomenon. At length the nucleus is seen to be elongated and it ultimately divides, and the two new nuclei rapidly separate; the constriction then becomes deeper and deeper, and in a few minutes the cell is divided completely by it. The process is precisely similar to that which has been described in the agamic division of the Infusoria.



FIG. 17 bis.—Blood corpuscles (*leucocytes*) of the adult larva: 1, living corpuscles, showing the amoeboid condition, in *d* the nucleus is also amoeboid; 2, the same, treated with magenta, showing the various appearances produced by the action of the reagent; 3, a living cell in several stages of direct division (all drawn with  $\frac{1}{2}$  oil immersion lens).

The blood corpuscles of the resting larva, nymph and imago, when fixed by steam and properly stained, sometimes exhibit distinct but irregular nuclear figures—asters, diasters, etc.—and several nuclei are frequently seen in one cell; hence it might be inferred that karyomitosis occurs in the division of the nucleus, as above described, although the conditions of the observation are such that this could not be seen in the living corpuscle.

The method I adopt for the examination of the nuclear figures

of blood corpuscles is Schäfer's.\* The blood is spread in a thin layer on the cover-glass, and fixed by holding it in the steam of boiling water, or passing the cover rapidly through the flame of a spirit-lamp. In this way the corpuscles may be fixed in the amœboid condition. The preparation is then stained by putting a drop of Ehrlich's hæmatoxylin on it for a few seconds. It is then washed rapidly with distilled water, and placed in hard water until the stain becomes blue, after which it is mounted in balsam in the usual way.

Some of these preparations are very beautiful, and exhibit both the intracellular reticulum, spongioplasm, and the intranuclear network, chromatin fibres. The appearances are precisely similar to those seen by Schäfer† in the white corpuscles of the newt. As in the newt, they frequently exhibit pyriform nuclei drawn out into long tails.

When the fresh blood of the larva is treated with a solution of magenta, the corpuscles swell up and discharge a granular mass, which leaves a perfectly transparent stroma around the nucleus (Fig. 17, 2, *g h i*).

H. Landois‡ and others have described crystals in the blood of Insects. Whenever I have observed crystals, I have always been able to trace them to some reagent used in the preparation. Staining with lithia carmine invariably gives rise to crystals of lithia salts. The same author states correctly that the blood plasma contains a globulin which is precipitated by  $\text{CO}_2$ , or acetic acid and other reagents. He also remarks that magenta produces the appearance known as 'Robert's macula.' Viallanes devotes a chapter to the consideration of the state of the blood of the larva immediately before its metamorphosis [27, pp. 131-136], which he summarises in the following manner: 'The cells of the blood of the larva are analogous to the leucocytes of Vertebrates, and are typical embryonic cells.'

\* Schäfer, E. A., 'On the Structure of Amœboid Protoplasm,' Proc. Roy. Soc., vol. xlix., 1891.

† *Ibid.*

‡ Landois, H., 'Krystallisation in Insectenblut,' Zeitsch. f. w. Zool., Bd. xiv.

**Phagocytes.**—It has long been known that amœboid blood cells are capable of enclosing molecular material, bacteria, etc., in their protoplasm, in point of fact, of feeding like amœbæ. During the histolysis of the larval tissues, the number of white blood cells rapidly increases, and many are seen with several nuclei. They are found surrounding, penetrating, or imbedded in the larval tissue in process of degeneration. These cells ultimately become loaded with globules of oil, and even with solid fragments of muscle. In this condition they were termed by Weismann [2] granule cells (*Körnchenkügelu*). He further distinguished large and small granule cells. The large ones Viallanes terms 'corps rosea.' They appear to be merely overgrown and loaded leucocytes (Pl. XVI., Fig. 4, and Pl. XVIII., Fig. 6). These are very numerous in the blood of the nymph, and some still remain in that of the young imago. The large granule cells are generally seen to be surrounded by young leucocytes, which appear to be feeding upon them, and some may be actually observed penetrating them by means of pseudopodia. It is clear to me that there is a continual transference of granules from cell to cell, those which are overloaded being attacked by younger and more vigorous leucocytes, which become granule cells, and are in turn themselves attacked by a succeeding generation of phagocytes, until the whole of the effete tissues of the larva are assimilated (see 'Histolysis of the Larval Tissues,' Chap. IX.).

**The Connective Reticulum** resembles the adenoid or retiform tissue of Vertebrates, and consists of a network of stellate branching cells and endothelial plates. It permeates the whole body cavity, and forms the subhypodermic cellular layer and the so-called peritoneal coat of the tracheæ and viscera. The smaller tracheal capillaries are excavated in the stellate cells of this reticulum.\*

\* The intracellular origin of the tracheal capillaries has been observed in the larvæ of Lepidoptera and Ichneumonidæ by Hermann Meyer, *Zeitsch. f. w. Zool.*, Bd. i. In Dipterous larvæ by Weismann [2]. In *Lampyrus* by Wielowiejski [138]. In the fat bodies of *Luciola italica* by Emery [139]. Under the

The best part for the demonstration of this tissue is the thin wall of the great abdominal air sacs, which is covered by a network of flat stellate cells. Tufts of branching cells, also belonging to the reticulum, are found on the terminal branches of the tracheal vessels, and sections exhibit it in the blood sinuses and between the muscles.

The evidence on which it is believed that this adenoid reticulum is developed from the parablast, although not direct in Insects, is on the whole very conclusive. It is precisely similar to the parablastic tissue of the Echinodermata and Cœlenterata described by Hertwig, Körtneff, and others. In parts of the body, more especially in the pericardium, it is converted into a true cytogenic tissue, from which amœboid leucocytes are developed. It is very abundant in the cœlom of the nymph, and is apparently formed by the metamorphosis of the leucocytes, which abound at this period, and the corresponding tissue in the larva originates from the deep cells which lie beneath the blastoderm, and not from the cells of the cœlomic pouches. Lastly, Schäffer [131] has traced the development of leucocytes to the peritoneal coat of the tracheæ, and to groups of cells closely related to, and probably merely a part of, the fat bodies.

**The Fat Bodies** of the larva have already been described (p. 85). Those of the imago are subcutaneous groups and strings of multinucleate cells.

Three kinds of cells have been described in the fat bodies of many Insects—Fat cells, Intercalated cells (*Eingesprengte Zellen*, *Oinocytes*), and Cytogenic cells (*Blut-heerde*).

The fat cells of the larva become cytogenic in the pupa, but whether from the immigration of leucocytes which multiply in their interior, or by actual proliferation of their nuclei, is a matter which cannot be definitely settled (see Chap. IX.). In the Blow-fly larva the oinocytes appear to be distinct from the

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skin of *Corethra* larvæ by Wielowiejski, Zool. Anzeig. 6 Jahr 9. A typical example of the formation of intracellular canals is seen in the development of the capillaries of Vertebrates, and the tracheal capillaries of Insects are developed in a precisely similar manner.

fat bodies, nor are the true cytogenic cells connected with them, as they are according to Schäffer [131] in the larvæ of *Lepidoptera*.

The multinuclear cell chaplets, which occur in both the larva and imago, are closely related to the fat bodies. Those of the imago at least appear to be young fat bodies, and the oinocytes of the imago are probably fat cells, the fat granules of which have been absorbed for the nutrition of the great food-yelks (eggs) in the mature female.

Recently the origin of the fat bodies in Insects has attracted considerable attention, owing to its import in relation to the parablaster theory. C. Schäffer has, I think, satisfactorily traced the development of the larval fat bodies in the Blow-fly to the peritoneal coat of the tracheal vessels, but both he and Graber also trace them in various insects to the hypodermic layer of the integument. I think, however, the figures given by these authors indicate that they had not to do with young fat bodies, but with tangential sections of the hypodermis. Both authors regard the cellular layer of the tracheæ as also of hypodermic origin, and as due to invagination, a view which I regard as untenable (see Tracheal System).

**The Fat Cells of the Imago** differ from those of the larva (p. 86) in being frequently multinucleate. Bütschli [126, p. 558, Pl. xxvii., Fig. 43], Claus,\* and Bolles Leet† concur in deriving them from multinucleate cell-chaplets similar to that described by Weismann in the larva; and my own researches lead me to the same conclusion, except that the great cell-chaplet of the larva certainly undergoes histolysis in the pupa, although other and similar chains of multinucleate cells appear in the young imago, and ultimately become fat bodies.

The fat cells of the imago are loaded with fat granules, and appear very similar to those of the larva, except that they are smaller. These cells usually exhibit a single vesicular nucleus.

In the immature state they are mixed with smaller cells,

\* 'Zeitsch. f. w. Zool.,' Bd. xxv., p. 266, Pl. XIV.

† 'Recueil Zool. Suisse,' tom. ii., p. 391.

some with two or four nuclei, in which fat granules are abundant. These are the proliferating cells from which the fat bodies are developed.

In the mature Insect, cell-capsules (mother cells), containing hardly any fat granules, or entirely exhausted, are seen amongst the fat cells, and contain a reticulum of stellate nucleated cells, closely resembling the segmentation cells of the food-yolk (Pl. XVI., Fig. 8).

**Intercalated Cells.**—The fat bodies of many Insects have peculiar pigmented cells scattered amongst the fat cells. Graber describes these as containing yellow or green granules and rod-like crystals, and he regards them as imperfectly developed fat cells. I have never found such cells in either the larva or imago of the Blow fly, unless the cell-capsules of exhausted fat cells (mother cells), which contain the stellate cells described above, are their representative. If this be so, Graber's 'eingesprengte Zellen' are more probably exhausted than imperfectly developed fat cells. I have not had an opportunity of examining the insects in which intercalated cells are described by Graber and others.

**Oinocytes.**—This term is applied by Wielowiejski to certain chains of cells which occur—a pair in each segment—immediately beneath the integument in the larvæ of some Diptera, which he regards as representing the intercalated cells of the fat bodies. This interpretation of their nature is, I believe, incorrect. Nor is the term 'oinocyte' a good one, as it has also been used for the intercalated cells of the fat bodies.

Wielowiejski says: 'The oinocytes in the Brachyceræ resemble those of Chironomus, and are situated in the same position, at the sides of the abdominal segments.' He

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The reader may consult the following papers on the origin and nature of Oinocytes (Wielowiejski), and Intercalated cells, Schaltzellen (Leydig):

137. GRABER, V., 'Ueber den propulsatorischen Apparat. der Insecten.' Archiv f. mikr. Anat., Bd. xi.
138. WIELOWIEJSKI, H. RITTER VON, 'Studien über Lampyriden.' Zeitsch. f. w. Zool., Bd. xxxvii., 1881.
139. EMERY, 'Ueber die Leuchtorgane von *Lampyrus italica*.' Zeitsch. f. w. Zool., Bd. xl., 1884.

describes these as five extraordinarily large cells, four of which lie close together, commonly forming a rectangular cord, whilst the fifth is separated from the rest by a cell's diameter, and always contains two nuclei; the others have only one in each cell.

This description may be applied to the same organs in the larva of *Musca*, except that all the cells usually have two nuclei or more, and I am by no means clear that the number is constant. They undergo complete histolysis in the young nymph.

I am greatly tempted to regard these remarkable structures as the remains of segmental organs, similar to those of the *Chætopods* and *Peripatus*. Although their developmental history is unknown, Graber gives a figure [114, Fig. 128] of 'the lateral body cavity' of *Stenobothrus variabilis*, in which the cavity, *lb*, *lb*<sup>1</sup>, is apparently a segmental organ, and the cells, *g*, are, I suspect, *Wielowiejski's* oinocytes and represent the remains of a segmental tube.

### 3. EPITHELIA.

**Epithelial Cells** differ from those of the parablast in being developed directly from the outer or inner layers of the blastoderm, and in not exhibiting an amœboid stage. The individual cells are generally united by a scanty intercellular substance, termed cement substance. It is usual to distinguish the several varieties by their form, as tabular, or flattened, spheroidal and columnar cells. An epithelium may consist of a single layer of cells, when it is termed simple, or of several layers, when it is said to be stratified.

Many epithelial cells possess cilia, but such are never found in the *Arthropoda*.

The epithelial cells of *Insects* may be classed as chitino-genic, secreting, and absorbent cells, on the one hand, and sensory cells on the other.

The cells derived from the epiblast are chiefly chitinogenic; those from the hypoblast are secreting or absorbent. They

may be further subdivided into mucigenic and serous cells. The sensory epithelial cells are all epiblastic in origin and usually chitinogenic.

The epithelial cells of the embryo are distinguished by their small size and their arrangement in several layers. As the cells of these layers interlock, they cannot be termed stratified in the strict sense of the term; they may be termed transitional, according to the usual nomenclature, but it scarcely indicates their nature. I prefer to term such epithelia embryonic. In the Blow-fly, at least, this variety is only seen in the embryo, in the imaginal discs, and young nymph. The epithelia of the larva are remarkable for the rapid growth of the individual cells, which, as already mentioned, attain extraordinary dimensions in the adult larva. The epithelial cells of the imago are very variable in size, but are usually far smaller than those of the larva.

**Embryonic Epithelia.**—The cells are very small, rarely exceeding 5 $\mu$  to 6 $\mu$  in diameter, and are multiplied with great rapidity, probably by indirect cell division, although, from their small size, it is difficult to demonstrate nuclear figures. The appearance of the nuclei is, however, indicative of karyokinetic changes. The cells are cubical, columnar, or fusiform, exhibiting one or more thin cuticular laminæ on their free surfaces. They are glued together by a firm intercellular cement material.

**Chitinogenic Cells** (hypodermic cells).—The cells which lie beneath the cuticular epidermis of the skin, and those which form the subcuticular layer of the stomodæum and proctodæum, are the principal chitinogenic cells. The cells beneath the cuticular skeleton are properly termed the hypoderm. They are either flattened or columnar. Those of the larva have already been described (p. 37). In the imago the hypoderm cells are far smaller, and are either columnar or tessellated. The latter are usually found under the transparent syndesmoses, where no muscles are inserted. The cells into which the muscles are inserted are columnar. Those at the bases of the setæ are spheroidal, and large in proportion to the size of

the setæ; some at the base of the largest are gigantic. The cells which support the setæ are termed trichogenic.

Many of the epithelial cells beneath the cuticular skeleton disappear entirely in the adult imago, others persist, and some of these are pigmented with orange-brown or red pigment granules.

The cells beneath the cuticular lining of the stomodæum and rectum in the imago are tessellated, except those of the rectal papillæ, which are large, cylindrical, and probably glandular (see Rectal Papillæ).

**Mucigenic or Muciparous Cells** are found in great numbers in the metenteron. They resemble the goblet cells of Mammals (Pl. XVI., Fig. 13).

The absorbent cells of the alimentary canal are probably all mucigenic. They exhibit a more or less marked basilar border, which in many Insects is so distinctly fibrillated that it resembles a mass of cilia. This condition is well seen in some sections of the intestine of the immature imago of the Blow-fly, in which the basilar border splits into tufts, so closely resembling tufts of cilia that they might easily be mistaken for them, except that, when the living cells are examined, there is no movement. In the adult insect the basilar border is much thinner (see Alimentary Canal).

**Serous Gland Cells** are seen both on the free surface of the alimentary canal and in the salivary tubules in the imago. They are distinctly striated like the cells of the pancreas, or rod-like like those of the kidney in Vertebrates. The cells of the Malpighian tubules contain various granular substances, oil and pigments, like those of the vertebrate liver (see Malpighian Tubes). The cell-substance also frequently exhibits intracellular channels.

There are also small convoluted subcutaneous wax glands (see Tracheal System), the cells of which are very small, but loaded with fatty matter like those of sebaceous glands.

**Cell-fibrillation.**—The cells, which intervene between the muscles and the cuticular integument, of the long columnar variety, are often palisade-like and undergo longitudinal fibril-

lation, forming a kind of tendon. This fibrillation commences next the muscle, and eventually nothing is left of the original cell but a stellate core of protoplasm enclosing the nucleus, surrounded by tendinous fibres.

A similar transformation of the cells of an epithelium into fibrous tissue occurs in the proventriculus, but the fibres are much branched, and form a close meshwork comparable with that of the elastic cartilage of Vertebrates, except in the extreme fineness of the fibres, which more closely resemble those of white fibro-cartilage (see Proventriculus).

**Development of the Integument of the Imago.**—The epiblast of the imaginal discs is differentiated into two layers, a superficial one of small and a deep one of large cells. The larger epiblast cells from which the setæ are developed remain as the hypoderm, but the great majority of the cells of the superficial layer become chitinized throughout their entire substance, and ultimately so intimately united that all trace of their original limits is lost. They are transformed into cuticle, and form the superficial part of the exo-skeleton. As early as 1870 I pointed out that the epiostacoid layer, which I then termed the protoderm, is cellular in character. From more recent investigations, I have now no doubt I was correct, for the examination of a series of nymphs at the stage of development in which the setæ are being formed cannot fail to convince the observer that the cuticular external layer is formed from the epiblastic cells, not by the secretion of cuticular lamellæ, but by the actual conversion of the cells into a skeletal epidermis, under which a second layer of cells is developed, the true hypodermis of the imago, chiefly by the extension of the trichogenic cells of the epiblast beneath the smaller cells of the outer layer.

**The Cuticular Structures.**—The cuticular epidermis of the imago does not differ materially from that of the larva (see p. 9). Where the sclerites are dense, however, the laminated structure is less apparent or entirely absent. Such parts are also opaque and deeply coloured. Wherever the cuticular integument remains transparent, it is distinctly laminated, and

may even exhibit lines vertical to its surfaces, corresponding with the divisions between the subjacent cells.

Whether the cuticular layers of the skin, the dermal skeleton, is to be considered, as Leydig held, as an indurated exudation from the cells, or as a modification of the cell-substance, is a question which is no longer open to doubt. The direct conversion of the epiblastic cells of the nymph into cuticular tissue is perfectly obvious (see Development of the Nymph), and I suspect that the laminated endostracoid layers are also formed in the same way, as well as the internal cuticular membranes.

This view is further supported by the gradual thinning of the hypodermal cells as the cuticular layers are developed, and by the eventual disappearance of the hypoderm beneath the harder sclerites of the adult imago; by the manifest fusion of the bases of the cells and the delamination of the basement cuticle of the sericteria of the larva; by the sculpturing of the surface of the epidermis, and by the presence of minute and often complex setæ on its surface.

The formation of the branching setæ on the surface of the membranous parts of the proboscis is quite inexplicable on the hypothesis that the cuticular layers are formed by a fluid or semi-fluid excretion from the cells. The laminated structure of the cuticle is, it is true, sometimes unbroken by any indication of areas corresponding with those of the subjacent cells, but this is sufficiently explained by the manifest fusion of their bases, which precedes the process of chitini-zation.

Leydig regarded the epidermis as a fibrillated matrix, but, as far as I know, there are no indications of fibrillation in the dermal cuticle of Insects. In the Crayfish, however, the hypodermis is said to be fibrillated, but this fact is no argument against its cellular origin, as a similar fibrillation occurs in the wall of the proventriculus of the imago of the Blow-fly, and is undoubtedly the result of the fibrillation of the extremities of the epithelial cells of which it is composed.

In the larvæ of some Diptera the cuticle is divided distinctly

into fields corresponding with the cells from which it is developed, and this occurs when the latter are united by an intercellular cement. The existence of this cement-substance can be demonstrated by staining with silver nitrate.

**Pore Canals** frequently exist in the cuticle. The largest pass into the hollow setæ and transmit a process from a trichogenic cell; smaller, frequently branching, canals pass into papillæ, or are lost in the thicker parts of the cuticle. All contain undifferentiated processes of the cells, and may be compared with the dentine tubes of a tooth or the canaliculi of bone.

The cuticular lining of the stomodæum and proctodæum are thin and laminated; that of the rectum has papilla-like teeth and ridges on its surface in the vicinity of the recto-metenteric valve, and hair-like processes over the rectal papillæ. Cuticular membranes also line the tracheæ and invest the individual fat cells. The basement membranes, on which some epithelia rest, must also be regarded as cuticular lamellæ.

#### 4. THE MUSCLES AND NERVES.

##### a. The Muscles.

The **Somatic Muscles** of Insects exhibit three varieties, which Weismann [124] distinguished as larval muscle, leg muscle, and wing muscle. Although in their ultimate structure these three forms of tissue are precisely similar, the manner in which the ultimate elements are arranged to form fibres differs, so that except when examined with adequate magnifying power the general appearance of each is very dissimilar from that of the others.

In the larva each muscle consists of one or more large fibres. Each fibre has a distinct muscle-sheath, sarcolemma, and nuclei are seen at intervals between the sarcolemma and the muscle-substance. The muscle-substance exhibits distinct transverse striation, and, as Weismann pointed out, the fibres are precisely similar to those of Verte-

brates. Except in being colourless, they closely resemble the pale muscle fibres of Mammals.

The ordinary or leg muscles in the imago exhibit no proper sarcolemma, and have their nuclei arranged in the centre of the fibres. Their transverse striæ are more marked than in the muscles of the larva, and the fibres frequently exhibit the appearance of being divided into 'muscle cases' by transverse septa—'Krause's membranes.'

Each muscle consists of one or many fibres, either inserted in a bundle into a common apodeme, or on one or both sides of the apodeme in a penniform or bipenniform manner. More rarely the fibres are inserted into the integument through the medium of fibrillated hypodermal cells, which closely resemble tendons (Pl. XVII., Fig. 5, *b*).

The wing muscles, *sternodorsales* and *dorsales*, are softer than the ordinary muscles. Each consists of several giant fibres without any sarcolemma, but surrounded by tracheal vessels and epithelioid cells. Each fibre consists of numerous fasciculi of fibrillæ, separated from each other by numerous nuclei. The fibres are easily broken up into their constituent fibrillæ, and only exhibit the faintest indications of transverse striation. Leydig [123] described the wing muscles of *Dytiscus* as yellow, possessing but little solidity, and as very easily separated into their constituent fibrillæ. In the fresh condition the wing-muscles of the Blow-fly are so soft that they appear almost semi-fluid. They have a bluish-gray colour.

**The Visceral Muscles** of the Blow-fly are distinctly striated; those of the alimentary canal consist of fusiform (often branched) flattened cells, with a single large ovoid nucleus embedded in each cell. These cells are united into fenestrated laminae by an intercellular cement substance, and, except that they exhibit very distinct transverse striæ, they bear a close resemblance to non-striated muscle fibre.

The muscle fibres of the dorsal vessel differ entirely from those of the alimentary canal. The dorsal vessel consists of a muscular tube formed of very fine transversely striated fibrillæ, which branch and form a longitudinal network around the

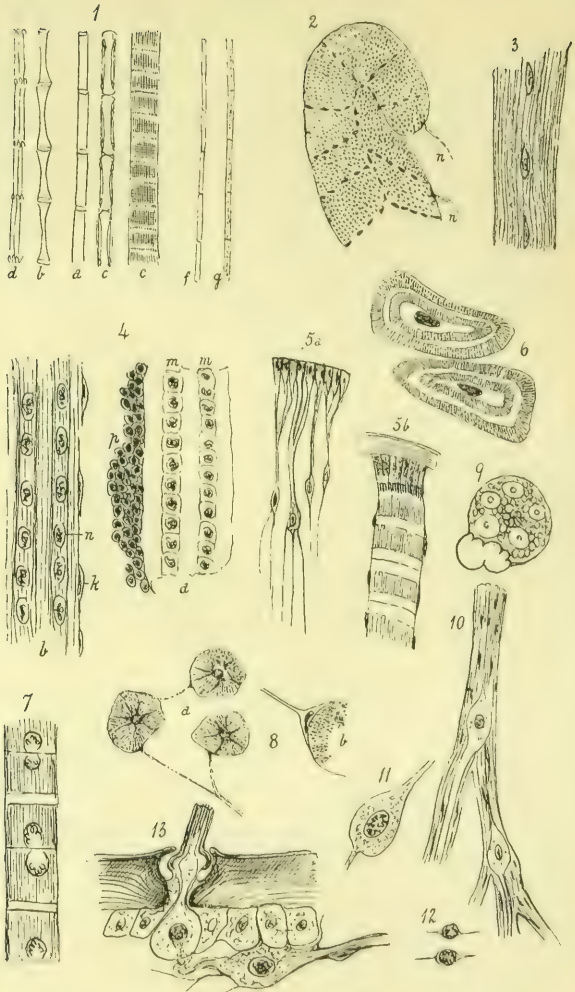
whole tube. Nuclei are seen at very regular intervals, one on either side of the dorsal vessel. According to Viallanes [27], it consists in *Eristalis* of a series of segments, each containing a pair of nuclei, one on either side. The segments are united by fine lines of cement material, which is stained by nitrate of silver. I have been unable to obtain definite results with silver nitrate either in the larva or imago of the Blow-fly, but I think it probable that the dorsal vessel consists of

#### DESCRIPTION OF PLATE XVII.

##### The Muscular and Nervous Tissues of the Fly.

- FIG. 1.—Sarcostyles: *a*, from the ordinary muscles; *b*, the same when stretched; *c*, appearances due to the overlapping of the sarcostyles when stretched; *d*, a portion of a muscle fibril, exhibiting longitudinal striæ and beads due to the overlapping of the sarcostyles; *e*, a fibril showing the so-called muscle-cases; *f*, sarcostyle from one of the great thoracic (wing) muscles; *g*, another sarcostyle from the same, showing a granular appearance, probably due to *post-mortem* change (all seen with a  $\frac{1}{2}$  oil immersion lens).
- FIG. 2.—A transverse section of a portion of one of the fasciculi of the great dorsal muscle: *nn*, nerve fibres ending in the muscle.
- FIG. 3.—A longitudinal section of a fasciculus of the same.
- FIG. 4.—Two stages in the development of the great dorsal muscle: *a*, an early stage, showing two rows of muscle cells, *mm*, and a group of parblast cells, *p*; *b*, a later stage, in which the fibrillation of the muscle has commenced (the muscle cells are fused); *n*, muscle nuclei; *k*, nuclei of the muscle-sheath derived from the parblast ( $\frac{1}{2}$  oil immersion).
- FIG. 5.—Tendon-like terminations of the muscles: *5a*, connective reticulum between the tergum and the young dorsalis muscle, from a nymph on the fourth day of the pupa stage ( $\frac{1}{2}$  oil immersion); *5b*, tendon-like insertion of an ordinary muscle from an immature imago.
- FIG. 6.—Transverse sections of ordinary muscle fibres near their insertion into the integument, showing a concentric arrangement of the muscle substance ( $\frac{1}{2}$  oil immersion).
- FIG. 7.—Karyokinetic figures and cell-plates in an ordinary muscle fibre, from a nymph on the twelfth day of the pupa state. The isotropous substance is seen to form broad bands between the cells ( $\frac{1}{2}$  oil immersion).
- FIG. 8.—*a*, Transverse sections of ordinary muscle fibres of the adult imago, showing nerve-terminals; *b*, a more highly magnified representation of the nerve-terminal ( $\frac{1}{2}$  oil immersion).
- FIG. 9.—A transverse section of the labial nerve of the proboscis, with a tracheal vessel attached to its sheath ( $\frac{1}{2}$  oil immersion).
- FIG. 10.—A similar nerve seen in the longitudinal section, showing the ganglion cells.
- FIG. 11.—A ganglion cell from the thoracic ganglion.
- FIG. 12.—Two small ganglion cells from the optic ganglion.
- FIG. 13.—A sensory seta showing the trichogenic and ganglion cells at its base. A process from the ganglion cell apparently ends in the nucleus of the trichogenic cell.

PLATE XVII.





such united muscle segments, an idea first suggested by Jaworowski.\*

**The Ultimate Structure** of all these forms of muscle exhibits a perfect uniformity of type. It is not my intention to give even a *résumé* of the very various accounts of the minute structure of muscle which are still under discussion. For details on this subject the reader may refer to the tenth edition of Quain's 'Elements of Anatomy,' in which he will find a good bibliography of the recent literature on the subject. The only memoir which agrees with my own observations is by Bütschli and Schewiakoff [134], and their results so completely accord with my own, that I shall give a *résumé* of them.

According to these authors, each fibre, muscle cell, or bundle of primitive fibrillæ, consists of two varieties of protoplasm—a contractile fibrillar substance and ordinary protoplasm, *intermediate substance*. The contractile fibrils, or *primitive fibrillæ*, are fine fibres with their long axes parallel to the long axis of the fibre. In transverse sections they appear prismatic, highly refractive dots, surrounded by the less refractive protoplasm, the intermediate substance or sarcoglia of Kühne. The transverse sections of the fibrillæ give rise to the appearance known as 'fields of Cohnheim.' The intermediate substance, sarcoglia or sarcoplasm, is distinctly reticular, but the reticulation is very irregular. The muscle nuclei are imbedded in this substance. The sarcolemma may be either a distinct membrane, as in the larval muscles, or merely a more or less condensed layer of reticular sarcoplasmic fibres.

Each contractile fibril is formed of two kinds of material, one anisotropic, the other isotropic. The anisotropic substance consists of prismatic or strap-shaped segments; these are united in a linear series by the isotropic substance, which they regard as a cement material.

The authors quoted state that the primitive fibril, contractile substance, is also reticular. Their figures are, however, more readily understood than their description, and it appears that the prisms of anisotropic substance are formed by still

\* Sitzungsbericht, K., Acad. Wien, Bd. lxxx., 1879.

smaller elements united together. The anisotropic substance is readily stained, the isotropic remains unstained, by carmine and aniline stains.

I shall use the nomenclature adopted by Schäfer [136], and term the primitive fibrillæ sarcostyles. Each sarcostyle (Pl. XVII., Fig. 1) consists of a series of sarcomeres, anisotropic substance, cemented together by a cement material, isotropic substance. A fibre consists of a number of sarcostyles, imbedded in a more or less abundant intermediate substance, in which the muscle nuclei lie. This I regard as the undifferentiated reticular protoplasm of the muscle.

With regard to the alleged structure of the sarcomeres, I have made many preparations from the wing muscles, in which they are most easily isolated, and it appears to me that each consists of a highly refractive flat or prismatic rod, in which I have sought in vain for evidence of more minute structure. It may be, however, that the means at my disposal are inadequate for any further resolution of structure, and as in every other point my observations entirely agree with those of Bütschli and Schewiakoff, I only wish to record the fact that I have been unable to resolve the sarcomeres, as they have done, into more minute constituent rods. My rod-like elements, sarcomeres, measure  $\cdot 001$  mm. in diameter, and from  $\cdot 002$  to  $\cdot 006$  mm. ( $2''$  to  $6''$ ) in length, whilst the ultimate elements described by the authors named are only  $\cdot 0006$  to  $\cdot 0008$  mm. in length.

By teasing the wing muscles in Flemming's mixture, it is quite easy to isolate the sarcostyles, and it is only a little more difficult to attain the same results from the muscles of the larva. The ordinary muscles of the imago cannot be so separated, but the thinnest sections indicate that they only differ from the other forms of muscle in the small quantity of interstitial substance, and the greater density of the reticulum, which plays the part of a sarcolemma.

When the muscle fibrillæ are stretched, the sarcomeres become narrow in their equator, and they then appear strap-shaped (Pl. XVII., Fig 1, *b*).

Most of the appearances which have been described in striated muscle fibres are, I believe, diffraction phenomena arising from the super-position of many layers of sarcomeres; others arise from the coagulation of the sarcoplasm, or intermediate substance. To the first I attribute the bright dots and dark transverse lines, and to the latter the cracks which are seen in transverse sections, and the reticulated appearances described by C. F. Marshall in specimens prepared with gold chloride.\*

**The development of the ordinary Skeletal Muscles,** 'leg muscles,' of the imago is readily observed in the nymph and immature imago, and throws much light on the nature of the muscle fibrillæ. In the youngest state each fibre appears as a row of cells placed end to end. In some cases the cells are fused together into a multinucleated protoplasmic cord; there is at this period no trace of transverse striation. At a later stage the nuclei exhibit karyokinetic figures, and divide in a plane transverse to the fibre. A bright line, a cell plate, appears between the two demiasters into which the nucleus separates (Pl. XVII., Fig. 7). The fibre increases in breadth during this process, but the distance between the cell plates diminishes with each division. Fibrillæ next appear at the periphery of the fibre. The cell plates are Krause's membranes, and form the isotropous cement material of the fibrillæ, the cell substance between the plates being differentiated into sarcomeres; a portion remains undifferentiated in the centre of the fibre around the nuclei.

The superficial portion of the cell forms a kind of sarcolemma, which is more firmly attached to the cell plates than to the intervening material. The bulging of the peripheral portion of the fibre from the imbibition of fluid, formerly relied on as demonstrating that the membranes of Krause are true septa, is due to this fact.

The membranes of Krause, my cell plates, are not permanent; they disappear as plates, and are only represented by the isotropous material of the sarcostyles in the fully formed muscle.

\* Quart. Journ. of Microsc. Science, vol. xxviii., 1888.

Many of the muscle fibres exhibit two or three concentric layers of fibrillæ, especially at the ends of the fibres (Pl. XVII., Fig. 6), where these are separated by tendinous tissue derived from the hypodermis, into which they are inserted. The larval muscles are also developed from rows of cells, and are at first non-striated. I have not succeeded in seeing the manner in which the fibre is subsequently converted into bundles of sarcostyles.

The wing muscles are developed from rows of muscle cells, but these are at first imbedded in a mass of parablast (Pl. XVII., Fig. 4, *a*). During their development the nuclei of the muscle fibre disappear; but those of the parablast cells remain between the fasciculi. The origin and development of the wing muscles will be further considered in the next chapter.

#### b. The Nerves.\*

**The Structure of the Peripheral Nerves.**—My observations on the structure of the larger nerve trunks, from the centres to their primary divisions, agree with the description given by Waldeyer. Each nerve trunk is surrounded by a nucleated sheath (Pl. XVII., Fig. 10) continuous with the capsule enclosing the ganglion from which it arises. The sheath is subdivided by branching longitudinal septa. The spaces enclosed by these septa contain fasciculi of exceedingly fine nerve fibrils, which in transverse sections appear as dark specks surrounded by a granular fluid. The whole closely resembles a gray or sympathetic nerve from a Vertebrate, consisting of several fasciculi of fibrillæ. It may be described as a number of fine axis cylinders surrounded by plasma and enclosed in a connective-tissue sheath.

Viallanes [27], I believe, first noticed that the nerves of Insects contain nuclei at intervals, chiefly at the angles of

\* For a general description of the nerve centres, see p. 66. A more detailed account will be given in the chapters devoted to the nervous and sensory organs.

bifurcation, distinct from and larger than the nuclei of the sheath. These he named 'axis cylinder nuclei.' I have frequently been able to demonstrate the fact that these are really the nuclei of fusiform bipolar ganglion cells. On the proximal side of each cell the process is an axis cylinder, but on the distal side it is a tubular nerve, which has some resemblance to a medullated nerve fibre (Pl. XVII., Figs. 9 and 10). Such large fibres are seen in transverse sections of the branches of nerves surrounded by fine axis cylinders.

Although the larger tubular fibres are blackened by osmic acid, they have far less fatty matter in their composition than the medullated nerves of Vertebrates. It appears to me that the proximal fibres should be regarded as nerve-root fibres, belonging properly to the central ganglia, whilst the larger distal fibres are true nerve fibres. At each bifurcation of the nerve one or more ganglion cells occur, so that the number of larger fibres increases. I regard the cells which appear at the angles of bifurcation as trophic nerve elements, similar to those of the ganglia on the posterior spinal nerve-roots of Vertebrates.

Whether all the nerve fibres, or only the sensory ones, pass through these ganglion cells is a matter on which I am still doubtful; but those which do, terminate in peripheral ganglion cells, the branching processes of which again assume the form of simple axis cylinders. I have not observed any such terminal ganglion corpuscles on the motor nerve fibrils which end in the muscle fibres. Hence I think it probable that all such large tubular nerve fibres are sensory in function.

Although I have compared the large nerve tubules with the medullated fibres of Vertebrates, I have never been able to find any indications of 'nodes of Ranvier,' or the rodded structure characteristic of the latter. The nerve tubules described by Weismann and others correspond with the large nerve fibres.

**Motor End Organs.**—I have sought in vain for well-marked motorial end plates both in the larva and the imago of the Blow-fly. The nearest approach to such organs are small, more

or less triangular specks of protoplasm, which is readily stained by carmine, immediately beneath the sarcolemma of the muscle fibre at the point at which the nerve enters the latter (Pl. XVII., Figs. 2 and 8). I have found it exceedingly difficult in my sections to demonstrate the nerve terminals in muscle at all, but in favourable sections have found a fine plexus of fibrils between the muscle fibres, from which branches pass into the muscle substance. In the imago the individual nerve fibrils are less than  $1\mu$  in diameter, but in the larva they are twice as large. In some sections it appears that the terminal nerve fibrils are connected with the transparent isotropous substance, but on this point I am by no means convinced, although the observation is in accord with the statements of Engelmann and Foetlinger. The well-marked motorial end plates, described and figured by Viallanes from the larva of *Stratiomys* and *Tipula*, appear to me to be the connective cells which exist on the terminal branches of tracheal capillaries, and I strongly suspect that the so-called motor end plates described in various insects are in reality the terminal cells of tracheal vessels, which are readily mistaken for nerves.

**Sensory Nerve Terminals.**—The cutaneous nerves either end in ganglion cells or in special sensory organs. Their terminal branches are much larger than those of the motor nerves, and are distinctly tubular. Occasionally a distinct axis cylinder, which stains deeply with logwood or carmine, appears in transverse sections as a central point in the nerve cylinder.

The terminal ganglion cells on the sensory nerves frequently give off a process which enters a trichogenic cell, and either passes to its nucleus (Pl. XVII., Fig. 13), or ends in a granular crescent on one side of the cell. These crescents are precisely similar to the menisci or tactile discs described by Ranvier in the pig's snout. The terminal ganglion cells also give off processes which penetrate the hypodermis and end in pore canals in the cuticle. Such nerve-endings are readily demonstrated in the larva.

Some of the cutaneous nerves of the larva, instead of ending in a single large ganglion corpuscle, have a group of small gan-

glion cells near their termination (Fig. 12 *bis*, 3), and end in demilunes of granular protoplasm on the inner surface of the hypodermis. Beside the end organs of the special senses, which will be described hereafter, many of the cutaneous nerves terminate in remarkable fusiform bi-polar cells. One or several such cells are enclosed within a capsular prolongation of the nerve-sheath. The central pole of each cell is continuous with a tubular nerve fibre; the peripheral pole is prolonged as a highly refractive cylindrical process, which lies in the axis of one of



FIG. 12 *bis*.—1. A section of the terminal joint of the Maxilla, showing the eye-like organs; 2. A section of the eye-like organ ( $\frac{1}{12}$  oil immersion lens); 3. Endings of a nerve in the hypodermis, showing a peripheral ganglion ('à côtes de melon,' Viallanes)—all from the Blow-fly larva.

the transparent moderate-sized setæ so abundant on certain parts of the insect. Such sensory setæ are numerous on the prosternum and the lips of the proboscis. They are probably organs of touch. Many of these encapsulated nerve-end organs contain peripheral cells, which are smaller than the central fusiform cells, and are not apparently connected with the nerve. They are perhaps concerned in the nutrition of the end organs, and resemble the outer cells of the taste buds of Vertebrates.

## CHAPTER IX.

### ON THE DEVELOPMENT OF THE NYMPH IN THE PUPA.

DR. WEISMANN'S great work [2] on the after-development of the Muscidae was the first memoir on the subject which can be regarded in the light of a scientific exposition. When we remember the primitive modes of histological research which were then in use, and the unsettled state of the opinions entertained as to the manner in which the tissues of the animal body are developed, we must regard this memoir of Weismann's as one of the most wonderful records, if not the most wonderful record, of brilliant discovery which has appeared in

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#### Bibliography.

140. HEROLD, M., 'Entwicklungsgeschichte der Schmetterlinge,' plates, 2 vols., 4to., Cassel, 1815.
141. WEISMANN, A., 'Die Entstehung des vollendeten Insects in der Larve und Puppe.' Abh. Senckenb. Natur. Gesellsch., Bd. iv., 1863.
142. LOWNE, B. T., 'Notes on the Development of the Nervous System of the Annulosa,' Monthly Microsc. Journal, January, 1871, pp. 260, 261.
143. METSCHNIKOFF, E., 'Untersuchungen über die intracelluläre Verdauung bei wirbellosen Thieren.' Arbeiten aus dem Zool. Inst. zu Wien, Bd. v., 1883.
144. BARFURTH, D., 'Die Rückbildung des Froschlarvenschwanzes.' Archiv f. Mik. Anat., Bd. xxix., 1887.
145. KOWALEVSKI, A., 'Beiträge zur Nachembryonalen Entwicklung der Musciden.' Zeitsch. f. w. Zool., Bd. xlv., 1887.
146. See also Zool. Anzeig., Bd. viii., pp. 98, 123, and 153, 1885.
147. REES, J. VAN., 'Beiträge zur Kenntniss der inneren Metamorphose von Musca Vomitoria.' Sprengel's Zool. Jahrbuch, Bd. iii., Abth. f. Anat. und Phy., 1889.

Perhaps the most important paper on the subject since those of Weismann [2] and Ganin [34].

the whole range of zoological science in the present half of the nineteenth century.

The only observations of importance made previously to the appearance of Weismann's exposition occur in De Reaumur's seventh memoir in the fourth volume of his '*History of Insects*'; and as these appear to me to possess a very high interest in relation to the most recent views propounded by Van Rees, I shall give an abridged translation of Reaumur's statements. He says :

'I have spoken elsewhere of those worms which are nourished in the intestines of the horse, and which only leave them when they are about to be transformed into pupæ. These insects remain within the pupa-shell much longer than the *Flesh flies*, and are much longer in becoming flies. I opened the shell of some eight days after the transformation, and was able to withdraw the whole insect from the shell without injury. In these I could observe neither wings nor legs, nor any of the parts proper to a nymph; they presented the appearance of elongated ovoids. . . . Probably all those flies which form the pupa-shell from the larval skin undergo this metamorphosis previously to becoming nymphs. I term it the spheroidal or ellipsoidal metamorphosis.'

He continues : 'With much address and patience, one may convince himself that this occurs in the *Flesh flies*,' and 'the worms therefore pass through a metamorphosis which is additional to that which caterpillars and the larvæ of most of the four-winged flies undergo.' If we open the pupa-case of one of the *Flesh flies* five or six days after the transformation of the worm, we find a well-formed white nymph, provided with all the parts of a fly; the legs and wings, although enclosed in sheaths, are very distinct. The sheaths are thin, and conceal nothing. The proboscis of the fly is seen lying upon the corselet and the lips, the aguillon and its sheath are distinct; the head is large and well developed, and the compound eyes are very recognisable. But how has our insect quitted its second form, the spheroid stage, to take this third form, that of the nymph?

‘There is nothing more easy than to get a number of fly pupæ, and, after boiling them, to remove the pupa-case. In this way we can watch the progress of events. At the end of two or three days the very short legs project at the anterior extremity, and on the next day the wings appear; in another day the extremity of the proboscis, and afterwards the whole organ becomes apparent. The head first shows itself in those nymphs in which the legs have almost reached the posterior extremity of the abdomen.

‘I have recognised that it is not that the parts grow day by day, as the appearances would lead us to believe, but that they exist preformed, and the mechanism of their evolution is very simple.

‘I have already spoken of a cavity seen at the anterior extremity of the ovoid, which contains the exuviated hooks and darts (mouth armature) of the larva. I have observed a similar cavity at this stage in all insects which pass through the ovoid condition, and there is a little horn bearing a stigma at two opposite points of its margin. I conclude that these stigmata belong to the corselet of the fly, and the parts which appear day by day are really en-sheathed in the cavity at the anterior extremity of the ovoid nymph.

‘In order to prove that this is really the case, I press upon an insect in the ovoid stage in which the extremities of the feet only are seen, and succeed at length in suddenly producing a nymph. I achieve by pressure a result which requires several days for its accomplishment in the natural state of things.

‘The most essential parts of the nymph and the imago, the head, wings and legs, are therefore lodged in the body-cavity of the worm before its first transformation, each enclosed in its envelope; for when they appear each is so enclosed. It is as if all the parts were invaginated, like the fingers of a glove withdrawn into the hand.’

No doubt Reaumur believed, from the analogy of what he knew to be the case in the Lepidoptera, that the limbs—wings,

head, etc.—of the Fly are in a far more advanced condition within the larva than they really are; but the main point remains, he recognised the fact that the parts of the nymph are at first invaginated, and that their appearance on the surface is due to evagination. And, further, he recognised a distinct stage in the evolution of the nymph, when all these parts are invaginated, and when the whole organism appears to be little more than a simple sac, containing a fluid or semi-fluid material; I shall refer to this stage as the *pronymph*.

The observations of Reaumur quoted above agree very closely with those of Van Rees, and with the following statement which I made in 1872: 'As yet a complete series of investigations are wanting, but I have traced the steps of development sufficiently to allow me to state that the great procephalic lobes which exist in the half-developed embryo become folded inwards, and lie one on either side of the alimentary canal during the whole period of larval life. These involuted procephalic lobes—and they are nothing else—form a portion of the imaginal discs of Weismann, whilst the eyes, antennæ, and mouth organs are ultimately developed from cellular outgrowths at the bases of the same structures, just as they are in the Crustacea' [142]. The above is, I believe, the earliest notice of the invagination theory of the origin of the imaginal discs, which I think more recent researches have placed beyond a doubt.

The development of the imago within the pupa-case will be considered under the following heads:

1. The formation of the pronymph from the larva.
2. The development of the nymph from the pronymph; and
3. The development of the imago from the nymph.

The first two form the subject of the present chapter, to which a *résumé* of the third has been added. The details of the development of the various organs of the imago will, however, be more conveniently elucidated in the second volume of this work.

## 1. THE FORMATION OF THE PRONYMPH FROM THE LARVA.

*From the commencement of the pupa stage to the end of the second or middle of the third day.\**

**The Paraderm.**—I shall show hereafter that the whole integument of the nymph is developed from the epiblast of the imaginal discs, but after the larval tissues have undergone histolysis (see p. 22), and are converted into a cream-like pseudo-yelk, the imaginal discs, which are as yet concealed in their provisional capsules, are united with each other by a cellular membrane, which encloses the pseudo-yelk. Van Rees regards this as the larval hypodermis; but the larval hypodermis has long before undergone complete histolysis, and the cellular covering of the pseudo-yelk is a new formation of parablastic origin. It is a temporary structure, destined to be replaced by the epiblast of the discs. I have therefore termed it the *paraderm*.

**The Pronymph.**—The parablastic sac enclosing the pseudo-yelk is Reaumur's ovoid stage, my pronymph. When the paraderm has been replaced by the ectoderm of the discs, the nymph is fully formed, and takes the place of the pronymph. Moreover, a cuticular layer is shed at this period, constituting the pupa-sheath of Weismann, which corresponds with the hard covering of the nymph in the Lepidoptera and other insects with obtectate nymphs (see p. 20).

The changes which occur before the formation of the pupa-sheath correspond nearly with those which take place in the caterpillar before the ecdysis of the last larval skin, whilst those which occur after its formation correspond with the changes which take place in the chrysalis, or nymph stage of the Lepidoptera.

If these views are correct, Reaumur's idea that the Diptera

\* The dates from the commencement of the pupa stage given in this work are much longer than those given by Van Rees, but correspond pretty closely with those of Weismann's memoir. They are only approximate, as so much depends on temperature.

exhibit an extra stage not separated as distinct in other Insects is substantially justified. In the Lepidoptera the phenomena of histolysis are partly carried out in the larva and partly in the nymph, whilst in the Diptera they are completed in a much shorter time, and a new stage of development becomes manifest. In the Lepidoptera the imaginal discs are united before the larval skin is shed, whilst in the Diptera their union is delayed until the process of histolysis is almost complete.

**The Histolysis** of the larval tissues proceeds from before backwards, and from without inwards. It commences in the anterior segments during the resting stage of the larva, and is not complete in the posterior segments until after the formation of the nymph. The cells of the hypodermis and the muscles are first attacked. The separation of the hypodermis from the larval cuticle is the first change which occurs after the pupa state is assumed, and, like the histolysis of all the tissues, proceeds from before backwards. It is easy to remove the anterior segments of the pupa-case on the first day of the pupa, but it is not possible to remove the posterior segments of the case before the end of the second, without injury to the pronymph, as the larval muscles and hypoderm remain attached to the cuticle longer than those of the anterior segments.

#### a. Histolysis of the Larval Muscles.

Kowalevski was the first who actually demonstrated the manner in which the histolysis of the larval tissues is effected, but he was led to undertake the investigation by the writings of Metschnikoff [143] on intracellular digestion. All the observations made before Metschnikoff's great discovery of the part played by the white blood corpuscles, *phagocytes*, may be passed over in silence, as they have been completely superseded and shown to be erroneous by the investigations of Kowalevski, first published in 1884. All that was actually known before that date may be summed up in the following words. A number of large granule cells, called 'Körnchen kugeln' by Weismann, and 'corps rosea' by Viallanes, make

their appearance whilst the muscles and other tissues of the larva undergo disintegration. The change is preceded and accompanied by a great increase in the number of blood corpuscles, and the whole contents of the pupa, except the rudiments from which the imago is developed, assume the form of a white cream-like fluid, or pseudo-yolk, the cellular elements of which, granule cells, are similar to the cellular elements of the great food-yolk of Birds and Reptiles.

As my own observations confirm those of Kowalevski in almost every detail, I shall give the results of his investigations. He says :

‘ If we investigate the changes which are going on in the young pupa by sections, it will be seen that the muscles and other tissues are completely surrounded by the blood plasma, and that, more especially in the anterior part of the body, vast numbers of blood corpuscles, leucocytes, adhere to the muscles. Pupæ one or two hours old already exhibit indications of the penetration of the sarcolemma by these corpuscles. Generally some of the muscle fibres exhibit one or two leucocytes in their interior close to the sarcolemma, whilst others still remain without any. A few hours later many corpuscles are seen within the muscle fibres. Minute cracks then appear radiating from these cells, and processes of the cells or the cells themselves may be seen lying in these cracks. Soon afterwards minute fragments of the muscle substance are seen entirely imbedded in these leucocytes, which are thus converted into the well-known granule cells. There is never any difficulty in distinguishing the nuclei of the leucocytes from those of the muscle, as they are smaller and more spherical. New cells are now seen continually passing into the cracks, and the latter extend so that the muscle becomes more and more broken up. When the whole muscle is permeated by the leucocytes, these assume a spherical form and separate from each other. The sarcolemma has by this time disappeared; it is probably so perforated by the passage of leucocytes that it allows the fibre to fall to pieces. The muscle nuclei, which Viallanes believed to proliferate, are removed in the same way as the rest of the

muscle; they are surrounded and enclosed by immigrant blood corpuscles. Frequently, however, the nuclei remain after the complete histolysis of the fibre, and are isolated by the falling apart of the granule cells. In this case they lie free in the blood, but are ultimately seized upon and disintegrated by amœboid corpuscles. These nuclei, when enclosed within the leucocytes, lose their vesicular form and become converted into spheroid or ovoid masses of material, which stain deeply with carmine. The blood corpuscles attack the muscles with such energy that on the second day (third day) scarcely any remain which are not converted into granule cells. These, although loaded with angular and spheroidal pieces of muscle, do not cease to move by minute pseudopodia. Moreover, they continue to feed and attack the cells of the fat bodies.'

There are two points in the foregoing description to which I would add a few words from my own observations.

Kowalevski appears to think that all the leucocytes (phagocytes) enter the muscle and fat bodies from the blood; at least, he says nothing of their rapid multiplication within these tissues. Many of the leucocytes within the muscles and fat bodies contain from four to six or eight nuclei, and are evidently undergoing rapid proliferation.

The second point is in relation to the muscle nuclei. It is true these are frequently seen surrounded by a clear protoplasmic area in the substance of the muscle, or free in the blood; but I cannot convince myself that the areole is a phagocyte. It appears to me that the leucocytes attach themselves to the exterior of the nucleus and perforate its capsule by sending a pseudopodium into its interior, after which the nuclear fluid disappears, and the chromatin falls into a mass which exhibits no definite structure. The remains of the nucleus then pass into one of the adjacent leucocytes and disappear.

#### **b. The Histolysis of the Hypodermis, and the Formation of the Paraderm.**

Reaumur was acquainted with the fact that the transforma-

tion of the resting larva into a pupa (see p. 3) is accompanied by a separation of the hypoderm from the overlying cuticular layers. The changes which occur in the hypoderm have been variously described, and they are by no means easy to follow.

Weismann says, speaking of the third-day pupa: 'The thorax of the nymph is already formed by the union of the imaginal discs, but it is not, as one would expect, enclosed within the larval hypodermis. It lies immediately beneath the horny pupa-shell. The hypodermis and muscles of the thoracic segments have undergone degeneration and have changed into a fine granular mass, which mixes with the blood in the interior of the developing nymph' [2, p. 165]. Weismann, who believed that the hypodermis of the abdomen of the larva changes directly into that of the imago, gives no nearer details upon the subject.

In spite of this direct observation of Weismann's, which is perfectly correct, Graber [10, Bd. ii., Figs. 163 and 178] gives a well-known schematic representation, as the result of the observations of Ganin and Viallanes more especially, and represents the Fly-nymph as consisting of a simple abdominal cellular integument, the hypodermis of the larva, with a double thoracic integument, the larval hypoderm, enclosing the newly-developed thorax of the nymph. I may at once observe that this scheme is entirely erroneous.

The most recent memoir on the Metamorphosis of the Blow-fly is by Van Rees [147], and his observations agree in the main with my own, which only differ in this, that what Van Rees regards as the larval hypoderm I regard as a new formation, developed after the histolysis of the larval hypoderm, my paraderm.

Sections of the resting larva, and of the pupa in its earliest stage before a trace of colour appears in the cuticular shell, exhibit unmistakable histolysis of the hypoderm, the cells of which are invaded by leucocytes at an earlier period than even the larval muscles. All the phenomena described as occurring in the muscles likewise occur in the cells of the larval hypoderm. The degenerating cells are swollen, their protoplasm

becomes spongy and scarcely stains at all with hæmatoxylin, borax- or picrocarmine, and the vacuoles contain blood corpuscles and multinucleated phagocytes. The nuclei of the epithelial cells are large and contain a large quantity of clear substance in which a small reticulum of chromatin is imbedded. This subsequently gives place to a mass of readily stained material on one side of the nucleus. The nuclei appear to be perforated by phagocytes. During these changes the hypoderm becomes widely separated from the larval cuticle; and a very thin cuticular layer is developed on both its outer and inner surfaces.

Sections made from pupæ an hour or two older show that the whole pronymph is covered by a layer of cells, which differ from those of the larval hypoderm. These new cells, my paraderm, have far smaller nuclei, which are apparently solid. The cells are no longer spongy and vacuolated, and their protoplasm, unlike that of the degenerating hypodermic cells, stains intensely with hæmatoxylin and carmine. Like the latter, they lie between the two cuticular laminæ already mentioned. It is exceedingly difficult to trace the origin of the paraderm. It either originates from the leucocytes developed within the cells of the hypodermis, or the hypodermic cells undergo a complete rejuvenescence. This later hypothesis appears to me most improbable, and I regard it as almost certain that the paraderm originates from leucocytes, and is a true parablasic tissue, similar to that which Korotneff has described as investing the yolk in the egg of *Gryllotalpa* before the appearance of the epiblast. Indeed, I think some of my sections (Pl. XVIII., Fig. 4) show that the paraderm is formed outside the degenerating hypoderm, and consists at first of small but rapidly growing amœboid cells.

This parablasic layer is continuous with the pedicles of the imaginal discs, as Van Rees described it. I only differ from him in no longer regarding it as the hypoderm of the larva. It is gradually absorbed after the epiblast of the disc becomes, as it were, engrafted upon it; for during the subsequent growth of the disc the large parablasic cells disappear beneath it, so that

the small epiblastic cells of the disc itself take its place and form the body-wall of the nymph.

Although neither Kowalevski [145] nor Van Rees [147] recognised the differences between the larval hypodermis and the paraderm which they regard as the larval hypoderm in the pupa stage, Viallanes [27] says: 'The hypodermic cells have become thicker than they were in the larva; their contours are effaced, so that it is not possible to limit the extent of adjacent cells. The protoplasm is not only more abundant, but it has acquired a property not exhibited in the larva—it stains readily with carmine and hæmatoxylin. The nuclei are, moreover, profoundly altered.' Though there are inaccuracies in his description, I quote it to show that the changed appearance of the cells has been observed. These new cells are certainly not

#### DESCRIPTION OF PLATE XVIII.

The Histolysis and Regeneration of the Alimentary Canal, and the Structure of the Imaginal Discs.

FIG. 1.—A transverse section through the chyle stomach of a pupa four days old; *d e*, degenerating larval epithelium; *e e*, embryonic epithelium developed from the scattered histoblasts of Kowalevski; *f f*, elongated fusiform cells; *l l*, parablasic layer consisting chiefly of amœboid cells; *p h*, phagocytes feeding on the larval epithelium.

FIG. 2.—A transverse section of the rudimentary mesenteron of the nymph, from a pupa five days old: *d e*, degenerating larval epithelium; *e e*, embryonic epithelium of the chyle stomach; *f f*, fat body; *i*, intestine of the larva forming the so-called corpus luteum; *p p*, parablast forming the provisional wall of the new mesenteron.

FIG. 3.—Leucocytes from the pupa on the fourth day.

FIG. 4.—Hypodermis of the larva, from a pupa a few hours old, in an advanced stage of degeneration.

FIG. 5.—One of the imaginal discs of the abdomen from a pupa four days old: *cu*, larval cuticle; *d*, the disc; *p p*, the paraderm by which the larval hypodermis is completely replaced.

FIG. 6.—Large granule cells from a pupa five days old.

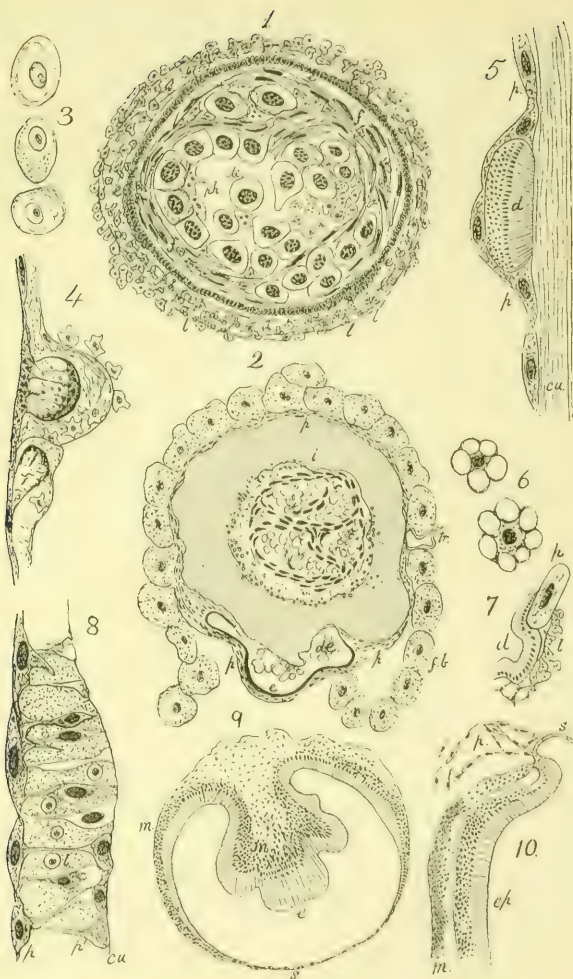
FIG. 7.—The edge of one of the wing discs from a pupa four days old, showing its relation to the cells of the paraderm and the amœboid cells, phagocytes, by which the latter is removed.

FIG. 8.—The paraderm from one of the intersegmental abdominal folds: *p*, superficial cells; *p'*, palisade-like cells; *cu*, inner cuticular layer (basement membrane); *l*, leucocytes.

FIG. 9.—A mesothoracic leg disc from a pupa about thirty hours old: *e*, epiblast; *m*, mesoblast; *s*, provisional capsule.

FIG. 10.—The edge of the wing disc from a pupa about thirty hours old: *e p*, epiblast; *m*, mesoblast; *p*, parablasic reticulum; *s*, provisional capsule.

PLATE XVIII.





thicker than those of the larval hypoderm, nor are the nuclei larger, as Viallanes states, but smaller.

Although transverse sections of young pupæ show that a considerable space exists between the pupa-shell and the larval hypoderm—which is filled by a serous fluid, and which remains for some hours after the paraderm is complete—the latter subsequently comes into close relation with the pupa-case, except at its anterior pole. This arises from the shortening of the pronymph, and is the result of the still further invagination of its anterior within its posterior segments. The anterior part of the abdominal wall, or, rather, of that part of the paraderm which has the abdominal discs attached to it, now forms a double fold, enclosing the parts derived from the thoracic segments. I term this the ‘anterior abdominal fold.’

The anterior abdominal fold is deepest on the ventral aspect of the pronymph, and is probably produced by the last contractions of the longitudinal ventral muscles of the larva. Subsequently the whole paraderm undergoes contraction with important results; for I regard this contraction as one of the essential factors in the evolution of the discs. Van Rees ascribes all the contractions which give rise to the definitive form of the body of the nymph to the larval muscles; yet these contractions occur at a time when, if any larval muscle remains, it is entirely detached from the integument of the pronymph.

Kowalevski actually observed slow but rhythmic contractions of the body of the pronymph after the whole of the larval muscles have been disintegrated by histolysis. I have no doubt whatever of the contractile power of the paraderm.

When the paraderm is completely developed, the thoracic portion of the pronymph is entirely covered by the anterior abdominal fold, whilst the cephalic portion is similarly invaginated within the thoracic.

### c. The Relation of the Imaginal Discs to the Paraderm.

I have already drawn attention to the true morphological character of the imaginal discs (p. 73). At the time I wrote

that section of my work I was unacquainted with the masterly memoir of Van Rees, and I would here remark that my conclusions agree so closely with his that, without this disclaimer, it might be supposed I had derived them from him without acknowledgment.

I shall perhaps do best to give a translation of the thesis which Van Rees supports in his memoir. After giving the history of the views of his predecessors, he says [147, p. 22]: 'It appeared to me that there is only one possibility which leads to a complete solution of the problem before us, that the imaginal discs are not only ectoderm, but are invaginations of the ectoderm itself. I can only understand the manner in which the Muscidæ are developed by supposing that the ancient progenitors of the Flies had imaginal discs, which, like those of the Tipulidæ, lay in immediate relation with the larval hypoderm; and that in later generations these were continually drawn more and more deeply into the maggot until they assumed their present positions.

'The fact that each imaginal disc in *Corethra* is supplied by a nerve and a tracheal vessel affords us a clue to the manner in which the relation of the discs to the hypoderm has been maintained. Although at length the imaginal rudiment may appear as a mere appendage of the nerve or tracheal vessel, it has nevertheless a neck or hollow pedicle closely applied to the nerve or trachea. This is readily seen when the neck is short, but in the extreme case we have probably to deal only with a difference of degree, and not of kind, so that we may conclude that the direct relation between the disc and the hypoderm is always maintained, and that the insertion of the pedicle into the hypoderm indicates the point where the disc must have lain in the ancestral form. The object of my researches has been to demonstrate this postulated connection between the disc and the hypoderm.'

Van Rees brings no embryological evidence to support his thesis, and merely remarks that he has traced the pedicles of the wing-discs into the hypoderm in the half-grown larva, in

which the pedicles of the leg-discs are more distinct than in the full-grown maggot.

As the discs of the wings and halteres are the only ones in which I have not succeeded in tracing any connection with the hypoderm, I am exceedingly gratified to find Van Rees places the connection on the same basis as that of the other discs by direct observation.

With regard to the function of the pedicles in relation to the evolution of the discs during the formation of the nymph, Van Rees has shown by transverse sections that the provisional cavity opens upon the surface by the shortening and ultimate opening out of the pedicle. His paper is illustrated not only by drawings of the discs at the period of their evolution, but by diagrams.

#### **d. The Contraction of the Paraderm and Evolution of the Discs.**

In the pronymph stage the imaginal discs all enlarge rapidly; their provisional cavities also become distended with fluid and extend into the pedicles. The latter become shortened, until at length the disc sacs lie in immediate relation with the paraderm.

A ring of small cells now appears at the junction of the disc sac with the paraderm in the position previously occupied by the pedicle, and the adjacent large flat paraderm cells begin to contract. The area of each cell diminishes and its thickness increases, so that the nuclei of adjacent cells are drawn together. At the same time an orifice appears in the centre of the small cells, which opens into the disc sac, and this rapidly enlarges, so that these sacs are converted into open pouches. The cells of the provisional capsules undergo the same contraction and thickening as the paraderm cells, a change which brings the disc to the surface. When this is complete, the provisional capsule becomes part of the paraderm.

The effect of the gradual but continuous contraction of the paraderm has been already alluded to. This contraction occurs chiefly, but not exclusively, in that part which corresponds with the abdomen of the nymph, where the evolution of the disc

epiblast takes place slowly. The paraderm of the thoracic region is removed during the rapid increase of the thoracic discs, which grow over its surface and subsequently unite with each other except on the dorsum; where the paraderm remains, however, the only covering of the pseudo-yolk long after the complete evolution of the head.

When the head is thrust forwards from the interior of the thorax, the cephalic discs are still in a very rudimentary condition, and are not united with each other except by the paraderm. Van Rees ascribes the evolution of the head and thorax to the contraction of the muscles of the larva before their final degeneration, but it is certain that these are in an advanced state of histolysis, and have lost all connection with the integument before it occurs. The evolution of the head and thorax is not, therefore, the result of muscular contraction, but of the organic changes which take place in the cells of the paraderm. These are slow and continuous, and the contraction of its surface, accompanied by increase in its thickness, continues until it is finally replaced by the ectoderm of the discs.

**e. Histolysis of the Tracheæ of the Larva and Development of the Tracheæ of the Pronymph.**

The tracheal vessels of the pronymph are developed from the anterior superior thoracic disc, which surrounds the spiracular trunk of the larva, and from the vessels already described (p. 85), which exist in the larva in relation with the imaginal discs, and exhibit an outer coat formed of small embryonic cells.

The greater part of the larval tracheæ undergo active histolytic changes; the external cellular coat is entirely stripped from them by the action of phagocytes, and the naked intima collapses.

The intima of the great longitudinal trunks is seen for three or four days lying in the pseudo-yolk. As Weismann observed, it is severed from its connection with the persistent portion of the tracheal system very near the anterior spiracle. It contracts to about half its original length, lies entirely in the

posterior half of the pronymph, and is ultimately withdrawn. It is found still attached to the cuticle of the larva around the posterior spiracles, on the inner surface of the pupa-case after the escape of the imago. Weismann supposed that the remains of the longitudinal trunks of the larva are withdrawn at the time the imago escapes from the pupa; but as these exuviae are entirely disconnected with the pupa-sheath and lie outside it, it is evident that they are expelled from the body of the pronymph before the pupa-sheath, the shed epidermis of the nymph, is formed. Indeed, I have found them in the pupa-shell freed from the body of the nymph on the third day of the pupa stage. The shedding of the tracheal exuviae appears to be dependent on the contraction of the abdominal paraderm, and to occur at the same time as the expulsion of the cuticular intima of the rectum of the larva from the pronymph.

#### f. The Histolysis of the Fat Bodies and other Larval Tissues.

The **Fat Bodies** during the formation of the pronymph separate into their component cells, so that the contents of the body cavity has the appearance of a granular fluid even before the histolysis of the muscles is complete. The fat cells, however, undergo histolysis very slowly, so that, as Weismann and Ganin observed, many persist even in the imago when it emerges from the pupa. The histolysis of the fat bodies commences, like that of the muscles, at the anterior extremity of the larva, and proceeds from without inwards, so that in the pronymph their cells are separated from each other, except where they are in immediate relation with the remains of the alimentary canal of the larva.

Kowalevski claims to have observed the immigration of the leucocytes into the fat cells in the following manner. He says: 'The breaking up of the fat bodies can be observed in the living nymph. I have several times withdrawn one from the pupa-case on the third or fourth day, and kept it alive in white of egg for more than twenty-four hours. The head vesicle is fairly transparent, and it is possible to watch the

disintegration of the contained cells. I saw small granule cells attach themselves to a fat cell and crawl over it; others subsequently made their appearance, so that two hours from the beginning of the observation the whole fat cell was covered by these leucocytes; indeed, in this state it resembled a segmented ovum in the morula stage. The appearance persisted for a long time, until at length a nest of granule cells entirely replaced the fat cell, and these finally separated and scattered themselves.'

I have not repeated this observation of Kowalevski's, and I am unable to understand how he obtained a satisfactory view of the process in the entire nymph. But I have taken living fat cells from the pupa, spread them over a thin cover, and fixed them with steam, subsequently staining and mounting them. Such preparations sometimes exhibit leucocytes in the act of entering a fat cell with remarkable clearness.

The changes which occur in the fat cells after the penetration of their external membranes by leucocytes are exceedingly interesting. At first a group of leucocytes is observed surrounding the nucleus; these multiply with great rapidity, and extend in ever increasing numbers outwards towards the cell-capsule. As the leucocytes increase in number, the fat granules gradually disappear and give place to vast numbers of cells, which differ in no perceptible manner from the blood corpuscles of the larva. The cells nearest the nucleus of the fat cells are far larger than those near the periphery, and the former are usually multinucleate. The latter probably originate by the division of the former.

During the process the envelope of the fat cell disappears, and eventually the peripheral leucocytes become scattered in the blood. For a long time after this the central larger cells cohere around the nucleus, but ultimately they separate and leave the nucleus, which, after a longer or shorter time, appears to be attacked like the muscle nuclei by phagocytes. Isolated nuclei are frequently seen free in the blood of the nymph, and these are usually full of cells which are set free as leucocytes Pl. XVI., Fig. 10).

Although in the foregoing description of the histolysis of the fat cells I have adopted the views of Kowalevski, it is by no means certain that this interpretation of the phenomena observed is the correct one. The fact that nests of leucocytes first appear around the nuclei and in their interior lends probability to a view long ago propounded by Arnold that in certain animal cells leucocytes are generated in large numbers within the nucleus. It is very difficult to distinguish between the emigration and immigration of leucocytes, and, although the idea that leucocytes enter the fat cells and multiply within them is perhaps more consistent with modern ideas, there is much to be said in favour of the view that leucocytes are formed within the nuclei and emigrate from them. Indeed, at one time I felt convinced from the appearances which I observed that this view must ultimately prevail, but at present I regard the question as an open one.

**Relation of Fat to Proteids.**—From a physiological point of view, the conversion of the cells of the fat bodies into nests of leucocytes is of great interest. Whatever the nature of the process may be, a large quantity of fat is converted into proteid material, probably by direct combination with substances rich in nitrogen. This much is quite certain, that the percentage of fat is very large in the mature larva, whilst little remains in the newly-formed imago when it escapes from the pupa-case. It is usually supposed that the fats are oxidized during the process of transformation, but in summer, when this is rapid, the loss of weight in the entire organism is very small, certainly less than 5 per cent. ; hence the fat cannot be accounted for in this way, and the rapid transformation of the fat cells into nests of leucocytes points to its actual conversion into proteid material. So long as we remain entirely ignorant as to the nature of this fat, it is hopeless to attempt any solution of the problem, and the source of the nitrogen which forms so large a proportion of the proteid is entirely unknown. Possibly highly nitrogenous extractives co-exist in the fat bodies with the fats which they contain. The subject would probably repay investigation by a competent physiological chemist, as

the relations of fats to proteids are far from being understood in man and the higher animals.

**Histolysis of the Sericteria.**—Much has been written on the degeneration of the cells of the lingual (salivary) glands of the larva, which are removed by histolysis on the third day of the pupa stage. Kowalevski describes the process as precisely similar to that observed in the muscles, and says that no organ exhibits it more beautifully. I have not been so fortunate in the investigation of this subject as Kowalevski, and, although I have no doubt that they are removed by phagocytes, I have not succeeded in obtaining such good preparations from these cells as from the muscles and fat bodies. It is well worthy of remark that the histolysis of these glands takes place at a later period than that of the other internal organs. This fact appears to me to indicate that the Muscidae are descended from insects in which the sericteria were concerned in the formation of a cocoon.

**Causes of the Immunity of the Imaginal Tissues.**—The question has often been asked why certain tissues, those proper to the larva, are attacked by phagocytes, whilst those which are destined to develop the imago possess an immunity to their action, although surrounded by them. It cannot be said that this question has been satisfactorily answered. Barfurth [144] came to the conclusion that those tissues only are attacked in which degenerative changes have already commenced.

Metschnikoff [143] observed that the leucocytes of a rabbit do not enclose the virulent bacilli of splenic fever, but that when the virus of these bacilli is modified by cultivation, they are enclosed by the same leucocytes in great numbers. He concluded, therefore, that the poison of the virulent bacilli protects them from the action of phagocytes, and, further, as certain poisons (*leucomaines*) are formed in living and functionally active cells, he postulates that the tissues destined to form the imago are endowed with such substances, and are so protected from the action of phagocytes. The theory is certainly ingenious, but would require additional evidence in its favour before it can be received.

Barfurth's idea at first sight has apparently more to recommend it, but there is no evidence that the muscles attacked are either feeble or dying, although they are no longer functionally active; and the metenteron of the larva, although functionally inactive, resists the attacks of leucocytes perhaps longer than any other larval tissue, and appears to be scarcely altered even on the third and fourth days of the pupa stage.

The theory that a chemical ferment exists in those tissues which are about to be removed and renders them capable of being invaded by leucocytes is equally unsatisfactory, as such ferments are soluble and could scarcely fail to infect the fluids and the body. I regard the subject as one on which speculations are useless.

#### g. Histolysis and other Changes in the Alimentary Canal.

The changes of the alimentary canal in the first days of the pupa state have been investigated by Ganin, Kowalevski, and Van Rees, and, although some discrepancies exist in the accounts they give, the following facts may be said to have been established.

The continuity of the cavities of the stomodæum and mesenteron is broken, and the posterior part of the œsophageal tube becomes an impervious cord. The crop is first contracted and then drawn into the œsophagus, and the cuticular intima of both the crop and œsophagus is shed with the pharyngeal armature of the larva. The muscular and cellular coats of the œsophagus and crop are subsequently removed by histolysis. The pharyngeal skeleton of the larva is withdrawn from the cephalic cleft in the pronymph, and a new stomodæum is developed.

Weismann [2] observed the gross changes which occur in the remainder of the alimentary canal. He says: 'Already on the second day the chyle stomach, which in the larva is more than 1·5 centimetres long, has become shortened to about '6 centimetres, and the openings of the Malpighian tubules, the boundary between the chyle stomach and intestine, are drawn forwards.' But, as Weismann shows in his figure,

there is no shortening of the alimentary tube behind the Malpighian vessels.

During these changes the Malpighian tubes become much paler in colour, and lose the nodulated appearance which is so characteristic of them in the larva, whilst their diameter increases considerably. The histolysis and regeneration of the chyle stomach advances rapidly in the pronymph stage, but the histolysis of the remainder of the intestine progresses far more slowly, and there are at this epoch no traces of its regeneration.

**The Histolysis of the Chyle Stomach**, according to Kowalevski [145], occurs in the following manner. 'The intestinal canal is entirely emptied in the resting larva, and its epithelium is altered in character; the protoplasm of the cells becomes homogeneous, no longer exhibits vacuoles, and the nuclei, instead of lying near their base, approach their free surface. The most important change, however, is the increase in the number of imaginal cells, which now form true imaginal discs. If we go a step further and examine the transverse section of a newly-formed pupa, the degenerating epithelium has lost its connection with the muscular wall of the tube, but, instead of lying free in its cavity, is surrounded by a thick layer of fusiform cells. The cells of this layer have nothing in common with the epithelial cells of the mid-gut; they originate from the same cells from which the new wall of the intestine is developed.'

It is in this view that I differ chiefly from Kowalevski. I think it extremely improbable that the fusiform cells originate from the imaginal elements, as they undergo complete histolysis in the nymph. Indeed, I am inclined to regard them as the remains of the muscular coat of the proximal intestine (Pl. XVIII., Fig. 1).

It will be remembered that the imaginal rudiments are only present in the chyle stomach, and it is difficult to understand the great shortening of the proximal intestine except on the hypothesis that it is invaginated within the chyle stomach. I have not been able to demonstrate this, but it will be seen

that a very thick layer of parablast surrounds the whole tube (Pl. XIX., *p*). The contraction of this layer is apparently the cause of the shortening of the gut, and probably not only causes the epithelium to accumulate in a mass, but also invaginates the muscular coat of that portion which has no imaginal cells between it and the epithelium, or, in other words, draws the degenerating and contracted intestine into the interior of the new layer of imaginal cells. The similarity of the fusiform cells to the muscular elements of the intestinal wall is certainly very striking.

The further development of the new mesenteron is one of the most extraordinary phenomena which occur in the pupa state. As it does not take place until the fourth or fifth day, it will be described in the next section.

#### **h. The Position of the Neuroblast and the Development of the Stomodæum of the Pronymph.**

The description given by Kowalevski of the manner in which the great crop of the larva disappears differs entirely from that of Van Rees. The Russian naturalist believed that it degenerates *in situ*. The statements made above agree more closely with those of Van Rees. Kowalevski's error originated by his not having observed the remarkable change which takes place in the position of the neuroblast at this period. The axis of the central nervous system, which in the larva is parallel with that of the body, turns through a right angle on the first day of the pupa stage, so that it is transverse to the long axis of the pupa, and transverse sections are no longer across, but parallel to the axis of the nervous system, the dorsal surface of which looks backwards, and the posterior extremity of which is ventral. At the same time there is a great increase in the size of the infra-œsophageal ganglia, which now lie in front of, and not below, the supra-œsophageal nerve centres (Pl. XIX., *s, t*).

The crop, when it is withdrawn into the œsophagus, forms a swelling which lies in front of and above the infra-œsophageal ganglia, which Kowalevski mistakes for the hemispheres, or

supra-œsophageal nerve centres. This change of position in the nerve centres makes it appear as if the crop still remains dorsal to the hemispheres in transverse sections until the real nature of the nerve ganglia upon which it lies is recognised; for the infra-œsophageal nerve centres, without careful examination in their new position and greatly increased development, are readily mistaken for the hemispheres. Van Rees, without remarking the changed position of the neuroblast, observed the withdrawal of the crop towards and afterwards into the œsophagus, whilst Kowalevski drew his conclusions entirely from an erroneous interpretation of the appearances presented by transverse sections.

Kowalevski derives the new stomodæum from the proventricular ring, Van Rees from a group of cells which appear at the point of invagination of the crop. My own view is that the remains of the larval stomodæum become invested by a layer of parablast; and that the new stomodæum is developed mainly from the embryonic cells which form part of the head discs, from the lingual discs which are seen on either side of the labium at the orifice of the salivary duct, and probably from the imaginal rudiments in the larval œsophagus, described by Van Rees, which I have not been fortunate enough to identify. These may possibly form the new crop, at first a short diverticulum of the œsophagus corresponding with the origin of that of the larva, which, it will be remembered, is a ventral diverticulum of the œsophagus, and not a dorsal one, as is generally believed.

I have already alluded to the discontinuity of the stomodæum and proventriculus of the pronymph. My sections of pupæ of the second day show no trace of the œsophagus immediately in front of the proventricular ring, and still further forward one comes suddenly upon the blind end of the degenerating œsophagus. This is surrounded by numerous parablast cells.

I strongly suspect that the blind posterior end of the œsophagus is connected with the proventriculus by a solid cord of parablast during the whole metamorphosis, although at this

early stage I have been unable to demonstrate the connection. In a later stage the solid parablasic cord uniting the blind end of the new stomodæum with the rudimentary proventriculus of the nymph is sufficiently apparent to leave no doubt in my mind upon the subject.

The development of the new stomodæum is by no means easy to trace, owing to the rapid changes which occur during the evolution of the head. According to Kowalevski, it is at first a wide, short tube, which only subsequently becomes narrow and elongated. Van Rees failed to observe its first stage, but it is evident that before the evolution of the head it must be a very much shorter tube than when the head appears in front of the thorax.

## 2. THE DEVELOPMENT OF THE NYMPH.

*From the end of the second day to the fifth day of the pupa stage.*

### a. The Position of the Imaginal Discs in the Pronymph.

The disposition of the imaginal discs in the pronymph is seen in Pl. XIX., which represents a vertical section in the median plane, from the rectum (*r*) to the neuroblast (*s*, *t*). In front of the neuroblast the section is taken through the discs, about 1 mm. to the right side of the median plane, except in the case of the wall of the œsophagus and the rudimentary mouth (*f*, *c*), which are shown in the median plane. Hence this figure is so far diagrammatic; it is a construction made from a series of sections, and not a drawing of any one section.

It will be seen by reference to the plate that the paraderm, represented by a double outline enclosing a series of short black lines, is invaginated above, and forms the roof of a cavity (*f*, *h*). This I term the 'cephalic involution.' Below and on either side of the cephalic involution there is a crescentic invagination of the paraderm, communicating laterally with the sacs of the

wing discs (*w*), and below with those of the leg discs (*i k l*). This I term the 'thoracic involution.'

The thoracic discs are still enclosed in the disc sacs, but these open into the cavity of the thoracic involution: those of the wings (*w*) above and laterally; those of the upper metathoracic discs, which are not represented in the figure, behind and below the orifices of the wing sacs; and those of the leg discs in order from before backwards on the ventral surface of the invaginated thoracic wall.

The anterior stigmatic (upper prothoracic) discs are at this period conical invaginations around the main trunks of the anterior stigmatic tracheæ of the larva (*c*).

The cephalic involution exhibits a roof which consists entirely of paraderm, and a floor composed chiefly of the cephalic discs. These are arranged in the following manner: In front of the stomodæum are the maxillary and lingual discs (*e*), with the orifice of the sericterial ducts between them. Above and behind the stomodæum is a tongue-like process (*f*), from which the pro-, meso- and metalabrum are developed. Behind and laterally are the antennal rudiments (*g*), and the optic discs of Weismann (*h*); the latter rest upon the hemispheres of the neuroblast (*s*).

It will be observed that all the imaginal discs are placed in

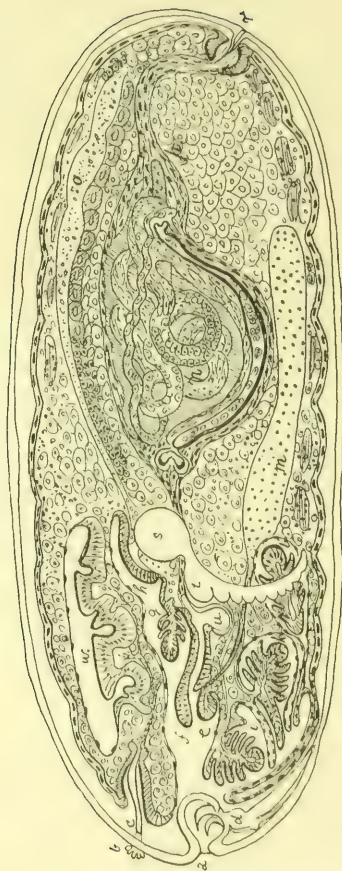
#### DESCRIPTION OF PLATE XIX.

A sagittal section of the pronymph on the second day of the pupa, constructed from a series of longitudinal and transverse sections. The section represents the median plane except in front of the neuroblast, *s*, *t*, where it is taken through the principal discs and gives the relation of the parts both in the median plane and about 1 mm. to the right of the median plane. The stomodæum is in the median plane, and the disc sacs in the plane of the anterior spiracles.

*a*, Cephalic involution of the larval integument; *b*, anterior larval spiracles; *c*, shed intima of the anterior spiracular trachea of the larva; *d*, mouth-armature of the larva; *e*, labial disc; *f*, labrum; *g*, antenna; *h*, optic disc; *i*, anterior leg disc; *k*, intermediate leg disc; *l*, posterior leg disc; *m*, sericterial gland of larva; *n*, cavity of the mesenteron of the pronymph, containing the intestine and Malpighian vessels of the larva; *o*, dorsal vessel; *p*, parablast surrounding the mesenteron, and connecting it with the rectum and stomodæum; *r*, rectum; *s*, hemisphere; *t*, ventral neuroblast; *u*, crop; *w*, wing disc.

The dark continuous outline within the chyle stomach of the larva represents the new epithelium of the mesenteron (compare Pl. XVIII., Fig. 2, *e*).

PLATE XIX.



FRONVMPH



the same relative positions as the parts subsequently developed from them; it is only the paraderm which is reversed by the invagination, its thoracic extremity being in front of its cephalic portion. As the rudimentary nerves and tracheæ of the nymph are all attached to the discs, no disturbance of their relations occurs during the process of evagination, and the reversal of the parablast, which is attended by its contraction, takes place without any disturbance of the internal organs.

**The Evagination** of the thorax, and afterwards that of the head, is undoubtedly effected by the contraction of the abdominal paraderm, which forces the pseudo-yolk forwards into the thoracic and cephalic cavities. As has been already observed, Reaumur came to the conclusion that the process is a mechanical one, and Weismann made the following remarks on the evolution of the head [2, p. 173]:

‘On the fourth day of the pupa stage the head is pushed forwards out of the hollow in the thorax in which the discs are developed; it then unites with the front of the thoracic integument. What the nature of the force is which produces the forward movement of the head may be subject to discussion, but I can assert with confidence that it is not the result of growth, but is purely mechanical. I once found the thorax well developed in a fourth-day pupa, but no head was visible; the latter appeared after the preparation had lain for some hours under the pressure of the cover-glass, although the nymph was of course dead.’

This is merely a repetition of Reaumur's experiment under somewhat different conditions. As Weismann, however, makes no reference to Reaumur, I think it evident that he was not at that time conversant with his memoirs. Reaumur, Weismann, and more recently Van Rees, have ascribed the evolution of the head and thorax to the contraction of the larval muscles before their final degeneration.

I think there is little doubt that the last muscular contraction gives rise to the shortening of the pronymph, by which it is drawn back in the pupa-case. This retraction releases the pharyngeal skeleton of the larva, which is subsequently found

depressed upon the ventral surface of the pupa-case in a dry and brittle condition. The formation of the anterior abdominal fold is also probably due to muscular contractions, but the reduction in the size of the abdominal region, which gives rise to the evolution of the head and thorax, is certainly not muscular. It occurs after the muscles are all completely detached from the body wall, and when most of them are in a far advanced stage of histolysis. These changes are clearly due to contraction of the paraderm, the cells of which increase in thickness as they diminish in the extent of their surface. Moreover, the character of the contraction differs entirely from the result of a muscular act. The reduction of the magnitude of the abdomen occurs very slowly, and gives it the form characteristic of that of the nymph. The anterior abdominal fold is obliterated and the thorax exposed, whilst the latter is subsequently distended, and the head is evolved by the flow of pseudo-yolk from the abdomen forwards.

#### b. The Development of the Integument of the Head and Thorax.

As has been already stated, the integument of the thorax is developed from the epiblast of six pairs of imaginal discs. The manner in which these overgrow and replace the paraderm has been described by Van Rees [147], and, except that he terms the paraderm 'the larval hypoderm,' my own observations confirm his statement that the edge of each disc overlaps the paraderm and extends by the development of new cells, whilst

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#### DESCRIPTION OF PLATE XX.

The exterior of the pronymph and nymph, and the anterior spiracles of the nymph.  
FIG. 1.—The thorax of the nymph at the end of the third day of the pupa, seen from its ventral surface (after Weismann).

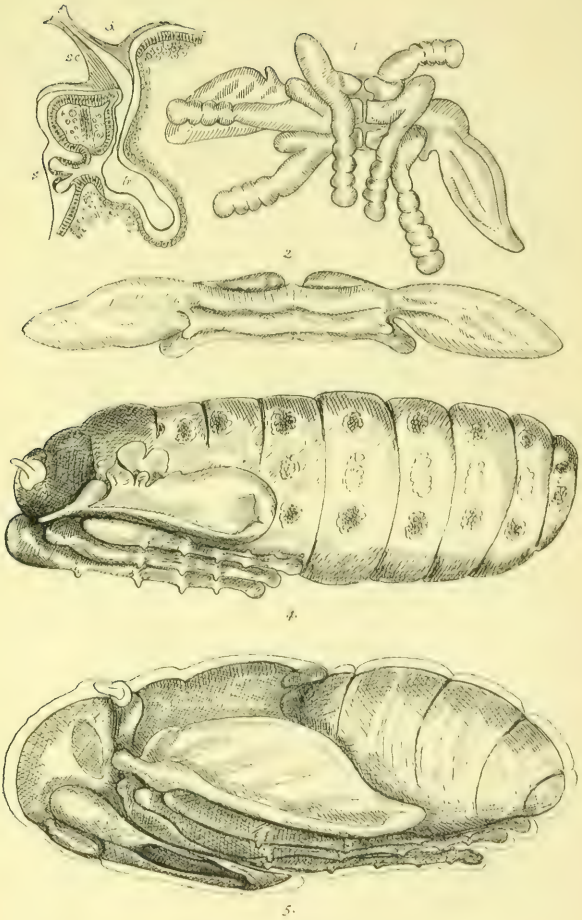
FIG. 2.—The same seen from its dorsal surface.

FIG. 3.—The anterior spiracular apparatus of the nymph on the ninth or tenth day of the pupa stage: *s* *c*, stigmatic cornu; *s*, intersegmental spiracle; *t* *r*, tracheal vessel.

FIG. 4.—The pronymph at the end of the third day, showing the position of the abdominal imaginal discs.

FIG. 5.—The nymph on the sixth day of the pupa stage.

PLATE XX.



PRONYMPH AND NYMPH.



the underlying paraderm is removed by phagocytes, which exist in great numbers near the edge of the growing disc.

During this extension, however, the disc also increases in size by the growth and multiplication of all its cells, whilst the paraderm undergoes a corresponding contraction in its whole extent. In this way the edges of the discs are ultimately united with each other, first in the ventral region, and later, on the dorsal aspect of the nymph.

**The Upper Prothoracic Discs** (Pl. XIX., *c* and Fig. 11) are seen as pouch-like involutions of the anterior edge of the cephalic involution, surrounding the shed intima of the prothoracic spiracular tracheal trunk of the larva.

These discs subsequently undergo evolution, *i.e.*, their inner surface, that next the shed intima of the tracheæ, becomes external, and they thus become the horn-like stigmata of the pronymph (stigmatic cornua). The rudimentary prothoracic tergum (dorsum of the prothorax), which is far larger in the pronymph than it is subsequently, is also developed by the extension of the edges of the anterior stigmatic discs (Pl. XX., Fig. 4).

**The Stigmatic Cornua** of the pronymph (Pl. XX., Fig. 3, *s c*) have a simple trumpet-like orifice, rapidly become highly chitinized, and acquire a yellow colour. They are subsequently shed, and are replaced by intersegmental spiracles developed between the pro- and mesothorax. These are the anterior spiracles of the nymph (Pl. XX., Fig. 3, *s*).

**The Intersegmental Anterior Spiracles** of the nymph resemble the anterior spiracles of the larva in having digitate extremities, but differ in possessing only four or five digitations. Weismann confounded them with the stigmatic cornua, and it is only recently that I discovered that the two are distinct and exist simultaneously.

The coexistence of two spiracles, one on, and the other behind, the prothorax, is of extreme interest, setting at rest questions as to the nature of the imaginal spiracles and the morphology of the thorax which have already been discussed, and bearing out the views I have expressed on the subject.

The **Leg and Wing Discs** are first exposed by the retraction of their provisional membranes. Their thoracic edges unite with each other in the median line of the ventral surface (Pl. XX., Fig. 1), subsequently from before backwards, and last of all on the dorsum. The appendages are developed as diverticula of the body cavity, which rapidly grow in length and diameter, and assume positions similar to those of the lepidopterous nymph (Pl. XX., Fig. 5).

The dorsal surface of the mesothorax (Pl. XX., Fig. 2) is completed by the union of the right and left wing discs. The upper prothoracic discs do not meet until the mesothorax is much enlarged, and the metathoracic discs remain separated in the median line above, or, if they meet at all, only do so by a narrow isthmus.

The mesothorax, when it is first closed dorsally, is a narrow ring no wider than the mesothoracic segment of the larva, but it increases rapidly from before backwards, and even at first exhibits a depression marking the future position of the post-scutal sulcus (p. 166).

The **Head** first appears in front of the thorax as a thin, bladder-like projection from its interior. As soon as it is entirely exposed, it is seen to exhibit five convexities, one lateral protuberance on each side corresponding to the optic disc and three median vesicles. The frontal vesicle is most prominent; it has the facial (antennal) vesicle on its ventral surface, and a narrow rim representing the occipital surface of the head, the posterior vesicle, above and behind it. The thin-walled head consists in great part of the paraderm of the cephalic invagination with the cephalic discs, which form a comparatively small part of its surface; for some hours after it appears in front of the thorax a great part of it consists of large flattened cells, very distinct from the embryonic epithelium of the disc epiblast.

**The Neck.**—The constricted neck is developed very slowly by the ingrowth of the parablastic layer, which forms a septum between the head and thorax. Sections through this region, and also those between the segments of the abdomen, exhibit

a remarkable palisade-like structure (Pl. XVIII., Fig. 8), which Van Rees has mistaken for the developing discs. The large cells of the paraderm give off processes and form new cells beneath them, which enclose a network of blood sinuses. These reticular septa are well developed between the abdominal segments when the discs are quite small, and they are not replaced by permanent structures until the development of the nymph is far advanced.

The **Proboscis** is developed from two median processes (Pl. XIX., *c* and *f*). The upper and larger of these, *f*, represents a layer of imaginal cells, which, in the larva, lie within the pharyngeal sinus (p. 44), and which is withdrawn from the sinus by the shedding of the cephalo-pharyngeal sclerite. It



FIG. 45.—A median section of the pupa on the fifth day, showing the proboscis, neuroblast, dorsal muscles, archenteron, and dorsal vessel of the young nymph.

becomes the pro-, meso- and metalabrum. The lower and smaller process, *c*, is formed by the coalescence of the four appendicular discs of the head (p. 82), and it is from this that the rostrum, pseudolabium and ligula are developed.

The maxillary discs (p. 82, Figs. 8, 2, *I*; 13, *mx*, and Pl. XV., Fig. 1, *i*<sup>3</sup>), which are first situated on the inner surface of the stomal disc of the larva, increase rapidly in size during the first few hours of the pupa stage, when they lie one on either side of the cephalo-pharynx. After the latter is shed, the discs unite with each other and with two small groups of imaginal cells, one on either side of the orifice of the united sericterial ducts, to form the lower median process, *c* (Pl. XIX.).

The small groups of imaginal cells at the orifice of the sericterial ducts represent the labium of the larva in which they are developed, and they form the ligula of the imago (p 147); hence, as has been already stated, I regard the pseudolabium, which is developed from paired maxillary discs, corresponding with the maxillæ of the embryo, as representing the galeæ of the maxillæ, and not the true labium, as is usually held.

On the fourth day of the pupa the mouth organs closely resemble those of an hemipterous insect (Fig. 45). The upper and lower processes lie upon the pectus and form a labrum and haustellum, between the basal portions of which the fulcrum is subsequently developed. The oral lobes do not appear at this stage, but are subsequently developed from the sides and apex of the haustellum, and by the seventh or eighth day the organ has assumed its definitive form (Pl. XXI.).

Weismann's account [2] of the manner in which the proboscis is developed is exceedingly indefinite. He says: 'Its several parts originate in a manner which is totally unlike that in which the mouth organs of the larva are formed;' and, after describing the origin of the latter from paired rudiments (lateral appendages), continues: 'The parts of the proboscis first appear in the pupa as structures similar to those which are ultimately developed from them; thus the underlip does not originate from paired rudiments, like the under-lip of the larva, but as a hollow, grooved process.' This is undoubtedly my lower process *e*, the origin of which I have traced to the coalescence of the paired maxillary rudiments. Weismann, moreover, admitted that he was unable to observe the earlier stages of the development of the proboscis.

Menzbier [50], on purely theoretical grounds, concluded that the head is developed from six pairs of discs, and he supposed that three pairs unite to form the proboscis; Künckel d'Herculais, as has been already mentioned, described the maxillary discs in *Volucella*, and these are the only facts which have been previously recorded as to the manner in which the proboscis is developed in the Diptera.

The **Antennæ** are developed as hollow processes of the great

head discs. Weismann says: 'The formation of the antennæ resembles that of the legs. First an oval furrow appears, which has a considerable extent and encloses an ovoid projection. The latter resembles the nucleus of the leg disc. Very soon three concentric furrows appear within it, so that the ovoid body is divided into three segments, the three rudimentary antennal joints.' And he adds: 'Even on the second day of the pupa the antenna has scarcely any resemblance to the developed organ.'

In Plate IV. the appearance of the antenna is represented in an advanced stage of the resting larva, on which Weismann relied for his conclusions. In a still younger larva, however, from which Fig. 13 was constructed, the antennæ are well seen in sections, and bear an unmistakable resemblance to the developed organs. The folds which surround the antenna at a more advanced period, and mask its true character, are developed from the part of the disc which becomes the face and forehead, and not, as Weismann supposed, from the antennal rudiment. These folds possibly form the two basal joints of the antenna, which are well seen in some of my sections on the second day of the pupa, when they are almost as large as the third joint.

In comparing the development of the antennæ with the legs, Weismann was probably biased by the belief that these organs are homologous with ventral appendages. The difference in the development of the two structures is very marked. The antennæ are first mere ridges of the head disc, enclosing the rudiments of the antennal nerves, and never become biramous at any stage of their evolution. Nor are they ever enclosed in separate provisional capsules distinct from those enclosing the optic discs.

**Changes in the Disposition of the Eye Discs.**—The eye discs in the resting larva (Fig. 13) lie in diverticula of the cephalic involution. Their corneal (outer) surfaces look outwards and forwards, and are covered by a provisional membrane. In the next stage the provisional sacs have become part of the cephalic involution, and the eye discs are thickened and plicated (Pl. IV.)

and form part of the wall of a great pyriform sac extending from the brain to the pharynx.

In the pupa on the third day they have become sacs, the corneal surface looks towards the interior of the sac, and is concave, whilst the outer convex surface is covered by an expansion of the optic stalk which unites them with the brain (see Fig. 46).

Van Rees finds great fault with Viallanes' figure of the eye disc, which represents it with the outer surface covered by a provisional membrane, and states that the surface which looks towards the exterior is covered by mesoblast. He has figured and described the discs in their third stage as they appear in the pupa, the concave corneal surface bounding the lumen of a sac. During the evolution of the head, the eye discs again become convex on their corneal surfaces.

Van Rees gives a perfectly correct description of the condition of the parts from which the head is developed, as they are found in the last larval and early pupa stages, but, had he examined them in a series of sections from larvæ a few hours younger, he would have found that Viallanes' figures are as correct as his own. He says: 'The forehead and eye discs of the adult larva extend from the brain, with which the latter are connected by nerve stalks, to the pharynx. The eye discs extend over the front of the brain and resemble mushrooms, whilst the antennal discs, which are continuous with the edges of the eye discs, at first form a tube and later a cone, with its apex attached to the pharynx.' This description scarcely differs from Weismann's.

#### c. Changes in the Neuroblast, and Development of Peripheral Nerves.

It is not my purpose at present to enter into the details of the development of the nervous system, which will be more conveniently given in a future chapter, but to present to the reader a review of the great changes which occur during the evolution of the neuroblast.

In the resting larva and pronymph the neuroblast increases rapidly in size, and, as already stated, its position varies at different stages of the development of the cephalo-thoracic discs.

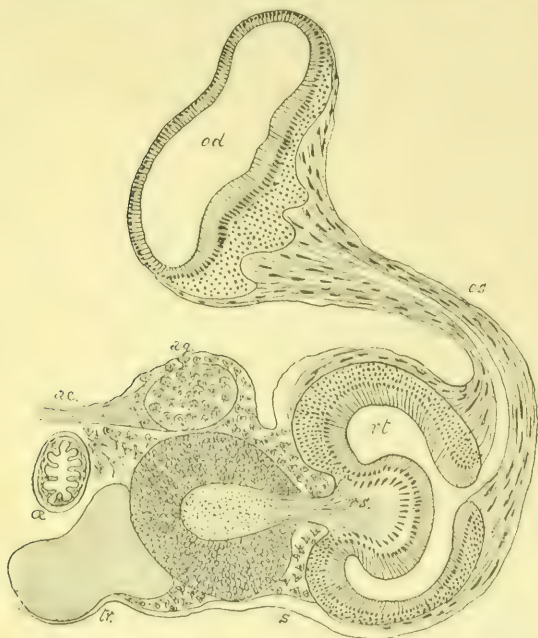


FIG. 46.—A semi-diagrammatic section of one of the hemispheres, the optic cup and optic disc from a pronymph on the third day of the pupa stage: *ac*, anterior commissure; *ag*, antennal ganglion; *od*, optic disc; *a*, oesophagus; *os*, optic stalk; *rt*, retinal disc; *rs*, retinal stalk, connecting the cup-like disc with the optic ganglion, which is seen surrounding its inner extremity; *tr*, trabecula.

During the evolution of the head discs on the second or third day of the pupa state, the hemispheres, which up to this period remain approximately spherical, become pyriform, and a groove

makes its appearance, dividing each into a proximal and a distal portion. The external or distal portion is larger, and subsequently develops the great optic ganglion and the retina of the compound eye; the smaller or proximal inner part becomes the supra-oesophageal nerve centre.

I have already referred to a remarkable epithelial disc, the retinal imaginal disc (p. 70) as it occurs in the larva (Fig. 13, *rt*), which has not been seen by any previous observer. A comparison of this disc with the cerebral vesicle of the embryo (Fig. 44) renders it probable that the disc cavity is the remains of the vesicle or part of the vesicle itself. Moreover, the disc cavity of the retinal disc is prolonged as a central cavity through the optic stalk (see Fig. 13 and Pl. IV.). In the pupa on the third day this disc has greatly increased in size, and its relations are represented in Fig. 46. In this stage it forms an optic cup, the inner surface of which ultimately becomes applied to the inner surface of the optic disc (*op d*), and forms the retina of the compound eye. This disc and its stalk, the optic tract, form the greater part of the external portion of the developing hemisphere. Sections through the optic cup and tract give very various and perplexing appearances, and it is only by a fortunate series that I was able to interpret its true structure. It will be at once apparent that tangential sections exhibit a closed sac, and, as the epithelial disc *rt* is folded and corrugated, some are not readily understood. Again, it is impossible to get a single section which shows the canal in the optic stalk and the retinal disc, as the optic tract is curved. It is not so difficult, however, to demonstrate the further evolution of the retina from the retinal disc.

As my own views on the structure and morphology of the compound eye are greatly at variance with those which are generally received, I must defer the further consideration of this subject until I give the full details of my investigations. In the meantime I would refer my readers to my published papers on the subject.\*

\* Lownc, B. T., 'On the Compound Vision and the Morphology of the Eye in Insects,' Trans. Linn. Soc., 2nd series, Zool., vol. ii., 1884. 'On the Structure of the Retina of the Blow-fly,' Journ. Linn. Soc. Zool., vol. xx., 1889.

The corpora fungiformia and antennal ganglia are differentiated from the inner or smaller portion of the hemisphere by the third day of the pupa, but the ventral cord between the infra-oesophageal and thoracic ganglia is not developed until the separation of the head and thorax is well advanced. Previously to the forward movement of the head these remain closely united with each other as in the larva.

Weismann [2] observed the pyriform condition of the hemispheres in the pupa, and described the manner in which they are divided into two parts by a groove; and Viallanes [27] has given many particulars on the changes which the optic ganglia undergo, and some of his observations and figures lead me to believe that, if he had not been misled by received views, which, as I have shown elsewhere, have no substantial basis, he would probably have discovered the manner in which the retina is developed in Insects.

Of the optic stalk (Stiel) which unites the optic disc to the hemisphere, Weismann says: 'It still appears on the fifth day of the pupa as a nervous cord, but on the twelfth day it can be no longer seen.\*' He concludes, however, that it has by this time spread out into an invisible layer over the whole surface of the ganglion. That he should have arrived at such a conclusion is scarcely consonant with the general careful character of his work. If, as he states, and as is certainly the case, the optic stalk disappears entirely between the fifth and twelfth day, the opinion that the radial striæ (which, he remarks, appear later between the optic disc and the optic ganglion) are the nerve fibres which existed in the eye stalk is not based upon any evidence, and appears to me contrary to the observed facts. My observations lead me to the conclusion that the whole of the nerve fibres of the optic stalk disappear, and that nothing remains but a thin layer of connective tissue, uniting the capsule of the optic ganglion with the edges of the optic disc, within which the retina grows outwards until its outer surface comes into contact with the inner surface of the parts developed from the optic disc—my dioptron.

\* These times refer to *Sarcophaga*, which is a week longer in the pupa than the *Blow-fly*.

**Development of the Peripheral Nerves.**—Weismann held it as probable that towards the end of the pupa stage, 'when the differentiation of the limbs into skin, muscles and nerves occurs, the newly-formed nerves come into relation with the limbs through the medium of the nervous portion of the imaginal pedicle.'

Van Rees states that in every stage of the pupa which he examined the nerves were demonstrable, extending from the neuroblast to the tissue of the discs. This is my own view of the subject, although in the early stages these so-called nerves consist in the main of formative tissue, cells and fibres, but contain no true nerve elements. It is very difficult to ascertain in what manner the fibres are developed, but it appears probable that they first appear at the central end of these conducting cords, and grow towards the limbs, etc.; but on this point I am guided entirely by analogy, and have at present no absolute evidence to offer. I hope, however, to have something more to say on the subject when I describe the nervous system, as I am at present engaged in some new researches on the subject. As, however, it is one presenting extreme difficulties, it is very probable that I may have to leave the development of the peripheral nerves an unsolved problem.

#### d. The Development of the Integument of the Abdomen.

Ganin [34] was the first to recognise that the abdominal integument of the imago is developed, like that of the head and thorax, from imaginal discs. He says: 'Weismann quite correctly states that the hypodermis of the eight abdominal segments of the larva is not destroyed, but he was wrong in supposing that the hypodermis of the larva is directly converted by the division of its cells into that of the imago,' a change which Weismann further states occurs at the end of the second or beginning of the third day. Ganin, it is said, discovered that the imaginal rudiments of the abdomen are already present from the first days of larval life; yet Viallanes says, 'According to Ganin, the hypoderm of the larva becomes transformed into

imaginal cells.' I am at a loss to reconcile this statement with the general tenor of Ganin's work.

Viallanes supposes that the larval hypoderm is destroyed before the discs enclose the pseudo-yolk. In this I agree with him, but only in a certain sense. Viallanes states that the pseudo-yolk is only covered by a fine cuticle before the discs grow over it. In this he was certainly wrong. Kowalevski, on the other hand, found that the discs grow over a cellular layer, which is only removed from the central area of the disc as its growth advances, and that they always overlap this layer by their edges. This view is also supported by Van Rees, but both authors regard it as the hypodermis of the larva. It is my paraderm.

**The Imaginal Discs of the Abdomen** (Pl. XVIII., Fig. 5, *d*) are two in number on each side of each segment, except the last, which only has a single pair of discs visible externally. The ventral pair lie one on each side of the anus, and are invaginated like the thoracic discs. This fact is noted by Kowalevski.

The position of the discs is well seen in Pl. XX., Fig. 4, which represents a very beautiful preparation made in the following manner. The pronymph was removed from the pupa-case, after heat-coagulation had been effected by boiling in water for a few seconds; it was immersed for three hours in a 0.1 per cent. solution of hydrochloric acid, transferred to a mixture of glycerine and water, gradually strengthened until it contained 50 per cent. of glycerine, and afterwards stained in borax carmine to which an equal volume of glycerine had been added. By this treatment the imaginal discs are the only part of the integument which receives the stain, and their limits are beautifully seen.

My specimen also exhibited a third and a larger more faintly stained region on each side of each segment, midway between the dorsal and ventral disc. These areas correspond with the large subcutaneous cells, which Wielowiejski termed oinocytes (see p. 276).

Van Rees believes that each abdominal segment has a third

dorsal disc on each side much smaller than the others, but I have found no trace of it. It cannot be doubtful that the two pairs in each segment correspond with the dorsal and ventral discs of the thoracic segments, from which they only differ in having no appendages and in their smaller size.

The union of the abdominal discs occurs from before backwards, and in the ventral median line, long before they unite in the dorsal region, so that even on the sixth day of the pupa the dorsal vessel can be seen pulsating beneath the transparent parablast, which still covers a considerable portion of the dorsal surface of the abdomen.

#### e. The Pupa Sheath.

On the fifth day the nymph may be regarded as completely formed. The wings, legs, segmentation of the body, and formation of the head, thorax and abdomen as distinct cavities, foreshadow the form of the imago, and resemble those of a lepidopterous nymph. But these parts exhibit, as it were, a rude outline of the perfect insect; the joints are as yet only indicated by furrows, none of the setæ are developed, and the embryonic epiblast of the imaginal discs has only partially replaced the paraderm in the dorsal region. The discs from which the abdomen is developed have not as yet coalesced with each other.

Amongst the small epithelial cells of the discs other and larger cells have made their appearance; these are the trichogenic cells from which the setæ are afterwards developed.

At this stage the whole surface of the disc epithelium is seen to be covered by a thin chitinous cuticular layer, which during the next day or two separates from the underlying epithelium, and forms a loose sheath, which is not cast off until the fly emerges from the pupa-case.

The formation of the nymph is, therefore, accompanied by two virtual ecdyses, that of the larval cuticle and that of the pupa-sheath, after which the cuticle of the imago is developed. Thus, as Weismann observed, 'we find three cuticular skins,

one over the other, in the ripe pupa—the pupa-case, the pupa-sheath, and the epidermis of the imago.’ The pupa-sheath is not, however, separated at once, but remains attached to the nymph at the inflections between the segments, and more especially between the head and thorax and the thorax and abdomen; it becomes greatly thickened in these folds before its final separation (see Pl. XXI.).

Weismann first described the manner in which the pupa-sheath is formed. Reaumur was aware of its existence, but he thought that the rudimentary appendages are enclosed in it on their first appearance. Weismann correctly stated that when they first appear on the surface they are not covered by any sheath.

#### f. Changes in the Alimentary Canal.

The changes which the alimentary canal undergoes in the first two days of the nymph stage (part of the third, fourth, and fifth days of the pupa) are of so extraordinary a character that I am greatly surprised to find that they had never been observed by anyone previously to my having undertaken their investigation.

Kowalevski correctly described the formation of a new epithelial layer in the chyle stomach by the union of the imaginal rudiments discovered by Ganin, but his investigations cease with the beginning of the third day of the pupa state. He gives a description of a section in which a new epithelial layer surrounds the so-called corpus luteum [145, Fig. 21], which he regards as the shed epithelium of the larval chyle stomach; but he fails to show what becomes of the remainder of the larval intestine, or in what manner the great saccular mesenteron of the nymph is formed.

There are 34 mm. of hind-gut, metenteron, in the larva, and 30 of these do not reappear in the imago, in which the metenteron only measures about 4 mm. Yet no one seems to have considered the impossibility of the total disappearance, not only of 30 mm. of intestine, but also of the great Malpighian tubes of the larva, without leaving a trace of their ever having

existed. By opening the pupa on the third day, or even after the legs of the nymph reach the middle or posterior third of the abdomen, it is easy to remove the whole alimentary canal, and it will be seen that the hind-gut is scarcely changed in length, and is almost exactly as it was in the resting larva, whilst the Malpighian tubules, increased in thickness and paler in colour, still exist, although their cells are much vacuolated and eroded. At this period it will be found that the intestinal coil formed by the metenteron and the Malpighian tubes lie in a cavity, bounded dorsally by the remains of the fat bodies of the larva and ventrally by the chyle stomach, which is strongly curved, its ventral surface convex and its dorsal surface concave (Pl. XIX.).

In sections (Pl. XVIII., Fig. 2) it will be seen that the chyle stomach is covered by a layer of parablast cells on its ventral surface, and that these cells connect it with the remaining lobe of the fat body and surround the whole intestinal coil, between the origin of the Malpighian tubules and the posterior three or four millimetres of the gut. The cavity bounded by these parablast cells also contains a quantity of coagulated fluid.

On the fourth day these changes are complete, and the chyle stomach is found to be split open on its dorsal aspect, so that its cavity is continuous with the provisional cavity in which the hind-gut and Malpighian tubes lie (compare Pl. VIII., Fig. 2, and Pl. XIX.). The cylindrical tube of new imaginal epithelium becomes thinner and thinner on the dorsal aspect of the chyle stomach, until at length it forms a crescent in section. The ends of this crescent grow upwards over the wall of the provisional cavity, and enclose the whole hind-gut and the remains of the Malpighian tubes, which form the so-called corpus luteum.

The posterior part of the metenteron at the same time becomes converted into an impervious cord of parablast, which connects the temporary mesenteron with the posterior extremity of the nymph. This cord is eventually contracted; thus it acts as a kind of gubernaculum, by which the new proctodæal rectum, formed by an invagination of the posterior segment of

the nymph, is brought into relation with the posterior extremity of a new metenteron formed by the elongation of the mesenteron of the nymph.

The nature and origin of the clear, coagulable fluid which surrounds the 'corpus luteum,' or degenerating larval intestine, is uncertain. It resembles blood, but contains no granule cells. The remains of the larval intestine are seen to be penetrated by and surrounded by leucocytes and multinuclear phagocytes, by which they are ultimately disintegrated. Crystalline substances resembling leucin and tyrosin are also frequently present at a later period. The fluid is absorbed during the later stages of development.

The chyle stomach, proximal intestine, Malpighian tubes, and metenteron of the imago are all developed from the archenteron of the nymph. (See Alimentary Canal of Imago.)

#### g. Origin of the Mesoderm.

**Mesenchyme and Mesoderm.**—Unfortunately, whenever a new term is introduced into science, it is years before it attains any definite meaning. A crowd of investigators seize upon it and apply it to every possible appearance which exhibits even a remote resemblance to that for which it was originally coined. Hence the most inextricable tangle of misconceptions originates. I shall not attempt to criticise the various meanings to which the term 'mesenchyme' has been applied, but to define the exact meaning I ascribe to it in these pages.

By mesenchyme, or parablast, I mean those groups of cells which have been at one time in their history wandering amœboid corpuscles, but which may form a continuous rete or network, or an epithelioid layer, and which are either converted into connective tissue, return to their amœboid form, or remain as amœboid cells. Whether these cells are budded off from the blastoderm, or whether they are the offspring of yelk cells derived directly as amœboids from the mother organism, may remain an open question; but that they exist in the food yelk is beyond doubt, and unless they become

connective tissues or endothelial cells, they are as a rule temporary structures, and form no part of the adult organism.

By mesoderm I mean cellular layers derived directly from the epiblast or hypoblast, or both, the cellular elements of which have never been wander-cells—amœboid corpuscles—and from which, as a rule, the muscular tissues are developed.

Whether there are muscle fibres which are developed from wander-cells is, I think, doubtful; but it is possible that there are, as Hertwig maintains.

**Structure of the Imaginal Discs.**—During the evolution of the imaginal discs, the details of their structure become far more apparent than in the earlier stages of their development, and since the issue of the first part of this work in 1890 I have seen good reasons for modifying what I then wrote concerning the nature of the mesoblast of the discs (p. 77). What I then regarded as mesoblast I now hold to be parablasic tissue.

In Plate XVIII., Figs. 5, 9, and 10, I have given details which were less distinctly seen in the younger discs which I then described. In the preparations represented it is perfectly easy to distinguish two layers of cells in the disc itself, a superficial layer of columnar epiblast and a deeper layer of small round cells, which I now regard as mesoblast, between the stellate parblast (which I formerly termed mesoblast) and the epiblast.

From a re-examination of the discs at an earlier stage, I have come to the conclusion that a thin layer of small mesoblastic cells is present even in the youngest discs, whilst the stellate parblast is certainly developed from wander-cells during their evolution in the pronymph.

Other groups of cellular elements are also developed during the evolution of the discs. Groups of outlying ovoid cells appear in the parblast around the tracheal vessels of the nymph. These have been described by Van Rees as the mesenchyme (mesoblast?) of the disc. I believe they are also parablasic cells, and that they are subsequently absorbed. Similar groups and strings of ovoid cells also appear in some sections between the stellate parblast and the small-celled

mesoblast of the disc, and extend into the parablast. I have as yet been unable to determine the fate of these cells, and am doubtful whether they are of parablasic or mesoblastic origin. I am tempted to believe, from their arrangement in strings, that they are developed from the mesoblast, and are rudimentary muscle cells; but as I am uncertain as to their nature I shall term them *intermediate cells*, from their position between the mesoblast of the disc and the parablasic plug which fills the provisional cavity.

The stellate parablast extends over the outer surface of the provisional capsule, and when the latter is distended by the development of the disc, ultimately entirely replaces its epithelial elements.

The various views which have been held as to the origin of the mesoblast of the discs are sufficient evidence of the difficulties which beset the investigation. I believe, however, that the recognition of the true character of the parablast, and its extreme importance in the developmental process, will do much to clear up many difficulties, and affords the clue to a reconciliation of many conflicting views.

Viallanes everywhere figures and describes my parablast as the mesoderm of the discs, and naturally arrives at the following conclusion: 'M. Ganin thinks that the mesoderm in each disc is derived from the exoderm, but a certain number of new facts lead me to think this is not general, but that in many cases *the mesoderm of the discs is formed from embryonic cells (blood corpuscles, etc.) scattered in the general body cavity.*'

Kowalevski, on the other hand, describes and figures my intermediate cells as mesoderm, and thinks they are developed from wander-cells. Van Rees entirely discards the term 'mesoderm' and uses the word 'mesenchyme.' He says: 'As matters stand, I must declare myself in favour of Ganin's hypothesis, and hold that this tissue arises from the cells of the epithelium of the discs. It is on this account that I use the term "mesenchyme" in the place of the old term "mesoderm," which is not only less definite, but incorrect, if we accept the views enunciated by the brothers Hertwig concerning its origin in their cœlom

theory.' What this means is beyond my comprehension, but it is clear to me that Van Rees' mesenchyme, in the regions from which the muscles are developed, consists of different elements, both parablastic and mesoderm cells. As to the origin of these cells, his opinions are, in my judgment, incapable of being maintained, as he has not been able to distinguish the mesenchyme (parablast) from the mesoblast. Neither do I regard his account of the development of the wing muscles as consonant with facts which have been repeatedly observed by myself and others. Whether Ganin really recognised the mesoderm as the inner disc cells, as his statement as to their origin leads me to think, is a question I cannot settle, as I am only acquainted with his work from the translations of Hoyer and others, as already stated.

#### **h. Development of the Dorsal and Sterno-Dorsal Muscles.**

Van Rees is of opinion that the dorsales and sterno-dorsales of the imago ('Brust Muskeln') are developed directly from larval muscles. The development of the muscular system of the imago has hitherto presented great difficulties, and the most diverse opinions have been held as to its origin. Weismann thought that the muscles are formed from granule cells; Künckel d'Herculais derives them from the discs; Ganin from the disc mesoderm; Viallanes retroverted to a view similar to Weismann's, and regarded them as developed from cells originating in the fat bodies; and Kowalevski returns to Ganin's view. In the face of the confusion which has arisen from not defining the exact meaning of mesoderm, it is very difficult to understand how far Ganin's and Kowalevski's views correspond. But it is clear that great differences of opinion exist on this point.

Van Rees, on the evidence of several sections of the pupa in the first day, which show three pairs of dorsal muscles of the larva in the second thoracic segment, in a less degenerated condition than those around them, concludes that these become the wing muscles (dorsales). Accepting all Van Rees' facts, it

appears that these muscles become surrounded by a vast number of cells, parablast or mesenchyme, and that this mass of cells persists and forms the nidus in which the wing muscles appear. There is nothing to show that one particle of the larval muscle remains. I am far from denying the facts alleged by Van Rees, but there is no question that the wing muscles are developed from mesoderm cells which grow from the mesothoracic disc, and that these grow into a mass of parablast. That this cellular parablast consists of leucocytes, which accumulate around certain dorsal muscles of the larva, is possible; but the larval muscle fibres described by Van Rees as the last to degenerate in the thorax form no part of the new muscles.

The dorsales and sterno-dorsales are at first minute and slender strings of cells imbedded in an abundant parablast. They first appear on the third day of the pupa state as six, not three, bands of cell tissue, chiefly parablasic in origin, of which nothing remains in the end except the nuclei, with, perhaps, some remnant of their protoplasm giving off long stellate processes, which form a connective reticulum for the support of the new muscle fibres. The development of the dorsales and sterno-dorsales in *Chironomus* can be distinctly watched in the living animal, and it is clear that, although developed between the fibres of the larval muscles, the latter take no part in their formation. I must hold, therefore, that the development of the muscles of the imago is not from those of the larva, although it seems likely that the vast numbers of leucocytes which surround these muscles may form coherent parablasic tissue into which the mesoderm cells of the discs grow. It may even happen, in the case of the wing muscles, that fragments of the larval muscles sometimes remain longer than in that of other muscles, although I have not observed the fact; but the new muscles neither originate from the nuclei of the old ones, nor in their substance by the transformation of existing muscle tissue. Neither do they arise from the leucocytes which surround the larval muscles. They are developed in every case from cells which grow from the discs themselves, and the parablast which surrounds these cells forms at most a connective

reticulum in which the muscles lie—a connective reticulum which, like the connective tissues generally, is, therefore, of parablasic origin.

### i. The Tracheal System of the Nymph.

The investigation of the changes which occur in the tracheal system in the nymph and pronymph stages is most difficult. The vessels are not easily traced in sections, in which of course no air remains after successful imbedding, and it is not until the nymph stage is far advanced that the tracheal vessels are easily demonstrated.

The earlier stages of their development have been described by Weismann, and the methods he adopted—those of ordinary dissection—although far from satisfactory, throw more light on the process than the newer methods of section-cutting. I am inclined to agree in most points with Weismann, but confess that I should feel more satisfied if my sections showed the conditions, which he described, clearly.

Such rough dissections as can be made bear out Weismann's statements, and the difficulty of tracing the tracheæ in sections in the early stages of the pupa is so great that, until some further methods of research can be invented, I fear little progress is likely to be made. In pupæ a few days older, however, the evidence of sections is unequivocal.

In the earliest sections of pupæ I have only found the large tracheal trunks in various stages of degeneration and re-formation, with an occasional group of small twigs cut through transversely, which are recognisable by their bright, highly-refractive intima.

Weismann says: 'The tracheal system of the pupa is very peculiar, and differs not only from that of the larva, but from every known variation of the respiratory system in insects. Only a small portion of the tracheæ of the pupa is formed in relation with those of the larva; the greater part is developed independently.

'Two great respiratory trunks are common to the larva and

pupa, but there is this difference, whilst those of the larva extend the whole length of the body and end in a stigma at each pole, those of the pupa are short and possess only anterior openings, the stigmatic cornua. From these the main trunks extend backwards for a short distance, and then suddenly break up into small twigs, which without further subdivision form a tuft comparable with a horse-tail ('Pferdeschwanz') and float freely in the pseudo-yolk' [2, p. 169].

It is these vessels which were first observed by Viallanes in the rudimentary wing, to which allusion has already been made (p. 160). They do not last long, but soon disappear, or only a small number remain, as I have sought for them in vain on the fifth or sixth day of the pupa.

Weismann adds: 'The main trunks in the nymph give off side branches, and are united in front by a transverse vessel.'

These are clearly the vessels to the several discs, and are developed from the tracheæ of the larva, which are distinguished by the small embryonic cells of their external coat (see p. 85 and Pl. IV.). The transverse commissure does not unite the main trunks, as Weismann thought, but the branches to the head discs, which become the anterior extremities of the main trunks of the nymph.

The separated intima of the larval tracheæ is shed by being withdrawn through the stigmatic cornua during their eversion, and remains attached to the pupa-case. Almost directly after this the intersegmental spiracle of the nymph is seen to be connected with a diverticulum of the wall of the main trunk close behind the stigmatic cornu.

During the separation of the pupa-sheath from the cellular ectoderm of the nymph, the intima of all these tracheæ separates from the cellular wall, a distinct space filled with fluid intervening, and soon after this a new intima appears outside the old one. This is the intima of the tracheæ of the imago.

The intima of the tracheæ of the nymph, the stigmatic cornua, and the intersegmental spiracles of the nymph separate with the pupa-sheath, but the shed intima of the tracheæ is not withdrawn from the tracheæ of the imago until the latter

draws itself out of the pupa-sheath as it escapes from the pupa-case.

**The Pro-imago.**—It is evident that the separation of the pupa-sheath and of the intima of the tracheæ is a virtual ecdysis. From this period the nymph becomes gradually transformed into the imago. I regard the nymph as completely formed as soon as this ecdysis has occurred, but as all the subsequent events are gradual developmental processes, it is impossible to say that either the nymph stage ends or the imaginal stage commences at any time, unless the actual ecdysis of the pupa-sheath and larval skin be regarded as the commencement of the imago state. To avoid circumlocution, it will be exceedingly convenient to term the nymph, from the shedding of the pupa-sheath to the escape from the pupa, the pro-imago, and to regard all those parts which exist at the time of the separation of the pupa-sheath as parts of the nymph, and all those subsequently developed as parts of the pro-imago.

For example, I shall speak of the tracheal system as it exists before this period of virtual ecdysis as the tracheal system of the nymph, and the new tracheal system which is subsequently formed as the tracheal system of the pro-imago.

#### k. The Dorsal Vessel and Cœlom.

The dorsal vessel of the imago is apparently developed directly from that of the larva. At every stage of development I have always found the dorsal vessel intact.

Herold [135] observed that in the Lepidoptera the pulsations of the dorsal vessel continue throughout the whole period of the pupa sleep. Newport confirms this in *Sphinx ligustri*, as he asserts that the vessel pulsates throughout the whole pupa stage, although its beats almost cease during hibernation, a period, however, in which development is also at a standstill. Künckel d'Herculais saw the heart beating in the pupa of *Eristalis* until the eighth or ninth day, after which he states that it stops or beats feebly for a day or two, but that afterwards it pulsates regularly.

Kowalevski [145] states that in the Blow-fly pupa it is seen pulsating on the third day as it does in the larva, but that later its pulsations are irregular, and he observed that the anterior and middle portions of the dorsal vessel remain almost unchanged during the whole pupa period.

Weismann, on the other hand, concluded that in the Muscidæ the dorsal vessel degenerates and is rebuilt in the pupa. He says: 'Although direct observations on the cessation of its pulsations have not been made, it may be concluded from its changes of histological structure that after a certain time contractions are no longer possible.'

'In the first days of the pupa state the dorsal vessel remains unaltered. The histolysis of the great tracheæ of the larva, to which its alar muscles are attached, removes its *point d'appui*. Its position is still, however, in the middle line of the back, although it is probably much folded by the shortening of the body of the larva. The ring (see p. 78), also degenerates on the fourth or fifth day, and removes its anterior attachment. The isolation of the vessel at this period is exceedingly difficult, as it has become very fragile, and is evidently in the first stage of histolysis. *As an organ, it is not broken up*, but is redeveloped by a similar process to that which has been observed in the intestine and Malpighian vessels.'

The main point to which I would draw attention in Weismann's statement I have printed in italics. The rest is not entirely accurate. The ring is not lost as a point of attachment, although it is profoundly altered. As an epithelial structure it no longer exists, but a vast number of cells appear around it before it disappears, and these cells form a dense network which remains apparent in the pro-imago, and is a conspicuous object in sections on the tenth day of the pupa, or even later.

This network of cells lies in the nymph above the hemispheres, and subsequently behind them, and appears to travel back over their surface as the head is developed.

The muscles which form the *alæ* of the pericardium are, it is true, removed, and a pericardium can no longer be said to

exist in the nymph; yet I see no reason to believe that the dorsal vessel ceases to pulsate, and in the numerous sections which I have examined I can see no evidence of any change in structure. It remains the same as in the larva until the last two or three days of the pupa state, and does not exhibit any traces of degeneration. Kowalevski says that when treated with osmic acid the boundaries of its constituent cells (muscle cells) become more distinct, and that its transverse striations are less marked on the third day of the pupa than in the larva. As, however, the demonstration of the muscle cells of the dorsal vessel by osmic acid is very uncertain at all stages, and the muscular striations vary in distinctness in different preparations, I am not inclined to regard the above statement as important, and Kowalevski leans to the opinion that the dorsal vessel does not undergo histolysis.

The last-named author erroneously supposed that the dorsal vessel is more deeply seated in the larva than in the pupa; in the posterior segments of the larva, as already stated, it is placed immediately beneath the integument. This portion is lengthened during the pupa stage, whilst the aortic section, which is deeply seated, becomes shortened.

Although I believe that the dorsal vessel persists during the whole period of the pupa sleep and performs its function, its form is so changed during the last few hours of this period that the dorsal vessel of the imago cannot be regarded as identical with that of the larva; and I think it probable that all its muscle cells are re-formed from embryonic cells, and gradually replace the muscle cells of the larval heart, since on the tenth or eleventh day of the pupa the dorsal vessel is lined by a double row of musculogenic cells, and from this period its lumen and the thickness of its walls rapidly increase.

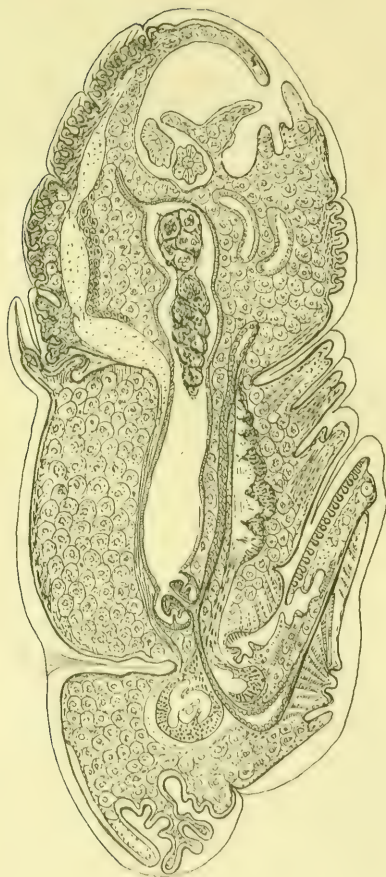
**The Cœlom, Cell Chaplets and Pericardial Cells.**—The cœlom in

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#### DESCRIPTION OF PLATE XXI.

A median sagittal section of a male nymph from a pupa seven days old, showing the relations of the nerve centres, dorsal vessel, stomodæum, archenteron, and recto-cloacal pouch. The cœlom is almost entirely occupied by cellular elements derived from the fat bodies of the larva.

PLATE XXI.



NYMPH.



the nymph is a continuous cavity between the body wall and the newly-formed alimentary canal, which contains the pseudo-yolk. It soon, however, becomes permeated by a parabolic network which binds together the alimentary sac and the embryonic rudiments from which the internal organs of the imago are developed. I believe this network is formed from the cells which cover the extremities of the young tracheal vessels.

The cell chaplets, which form the fringes of the dorsal vessel, and some at least of the great pericardial cells of the larva, remain and retain the same relative position as in the larva. The pericardial fringes grow rapidly by the multiplication of the cells of which they are formed. Their function and their ultimate destiny are, however, unknown.

Kowalevski [146] discovered that if the larvæ are fed with flesh impregnated with carmine, methyl blue, or silver salts, the pericardial fringes, the great pericardial cells, and the cell chaplet of Weismann become intensely coloured, and that the cells of the pericardial fringes remain coloured, not only during the whole pupa stage, but for some days after the imago emerges from the pupa. These cells multiply so rapidly, according to the above-named author, that they form a network which clothes the whole of the posterior part of the mesophragma. He also observes that the cell fringes of Weismann disappear soon after the histolysis of the salivary glands is complete, and that only seven pairs of pericardial cells remain in the imago. The six posterior pairs degenerate.

Flies fed with syrup coloured with cochineal, according to Kowalevski, soon exhibit coloration of the pericardial cell fringes.

I have frequently found pericardial cells in the nymph on the third day scattered amongst the constituents of the pseudo-yolk of the posterior part of the abdomen. These undergo histolysis like the fat bodies, and are probably the cells from the posterior part of the pericardium. The persistent pericardial cells are probably the elements from which the alar muscles of the pericardium of the imago are developed, as I find them embedded in the substance of their fibres.

### 3. THE DEVELOPMENT OF THE IMAGO FROM THE NYMPH.

*From the fifth day of the pupa state to the escape of the imago.*

The development of the nymph, as already stated, may be regarded as complete when the pupa sheath is separated from the subjacent cellular layer. From this period until the imago emerges from the pupa, the process of development may be conveniently divided, as Weismann [2] suggested, into two stages. The first commences on the fifth day, and terminates



FIG. 47.—A section through the abdominal integument of a nymph from a pupa seven days old: *cu*, outer cellular layer of small epiblast cells; *h*, inner cellular layer of hypoderm and trichogenic cells. The cuticular layers are developed between the outer and inner cells.

about the end of the seventh. During this period the external form of the nymph undergoes rapid evolution, and by the end of the seventh day differs but little from that of the young imago when it is ready to escape from the pupa-shell. The integumental setæ are developed from the large trichogenic cells, and the small cells of the epiblast between them increase in number so rapidly that the whole integument becomes minutely corrugated, the great setæ arising from the ridges. The hollows of the rugæ are occupied by minute setæ which

closely resemble cilia. These form the down-like hairs which cover the body of the imago (Fig. 47).

Subsequently the cellular integument is seen to consist of two layers of cells: a superficial layer of very small ones, which ultimately become converted into a chitinous membrane; and a deep layer of large cells, the trichogenic cells beneath the great setæ, and of medium-sized cells derived from them, which form the hypodermis and the deeper layers of the cuticle developed after the escape of the imago from the pupa (see p. 280).

The corrugation of the integument, which is especially marked in the abdominal region, permits of its expansion after the escape of the imago from the pupa-case.

By the end of the seventh day the articulations between the limb segments begin to assume definite characters, and the pads and claws of the tarsi are formed from their terminal lobes. The larger wing nervures are present as distinct ridges, and the oral lobes of the proboscis are so completely developed that the similarity of the mouth to that of the Hemiptera, so marked at an earlier period, is no longer obvious.

The second period, from the end of the seventh day to the escape of the imago from the pupa, is marked by scarcely any changes of external form, but is chiefly remarkable for the rapid development of the internal organs, which make very slow progress during the first period.

Throughout this second period the development of the contents of the head-capsule exhibits a marked advance over that of the thoracic and abdominal organs, and the contents of the thorax are further advanced than those of the abdomen.

Whilst the thoracic ganglia remain comparatively rudimentary, the brain exhibits great complexity, and scarcely differs from that of the adult. The least developed organs of the head, on the tenth day of the pupa, are the compound eyes, in which pigment first appears on the ninth or tenth day; but the simple eyes are already fully developed, and are apparently more perfect than in the adult imago. These organs in the pupa are more like the simple eyes of spiders than those of the adult insect.

The stomodæum and proctodæum are also far more advanced than the mesenteron; this on the tenth or eleventh day is a mere thin-walled sac, with a coiled cæcal prolongation of its posterior extremity, which becomes the metenteron. At the junction of the latter with the mesenteron the Malpighian vessels are seen as short cæca; they are chiefly developed during the last two days of the pupa stage, but the rectal papillæ are almost as well developed on the tenth day as in the perfect insect.

The thoracic muscles and ganglia are very imperfect at this period, and Weismann observed that if the nymph is removed from the pupa-case even on the eleventh day, it exhibits no trace of muscular movement. The great size of the blood sinuses and the late redevelopment of the dorsal vessel have been already referred to.

The tracheal system of the imago remains very inconspicuous until after its escape from the pupa, so that Weismann states that, 'of all the organs, the tracheæ are the last developed' [2, p. 235]. In this he was wrong, as the principal tracheal trunks of the fly are all present on the ninth or tenth day, although the smaller vessels are apparently developed later.

The sexual glands form a marked exception to all the other internal organs, as they exist in a rudimentary condition in the young larva, and probably in the embryo, and undergo progressive development, which is complete in the male a few hours after its escape from the pupa, and in the female, only some weeks later.

## APPENDIX TO CHAPTERS VI. TO IX.

### METHODS OF STUDY.

No great difficulties have been experienced by me in the preparation of sections of either embryos or nymphs, except in the early stages of the pupa, when the pupa-shell cannot be removed.

The difficulty in this case arises partly from the impermeability of the pupa-shell, partly from the fact that paraffin will not adhere to it, and partly from the extreme friability of the sections—perhaps due to the difficulty of fixing the tissues owing to the impermeability of the pupa.

In preparing embryos, it is advantageous to remove the chorion, or egg-shell, after heat coagulation, but I have prepared very good sections occasionally when this has not been done, staining them after cutting. I have found it impossible to stain them in mass unless the shell has been removed. Young pupæ should be divided with a razor after heat coagulation, and the extreme ends of the pupa case cut off. In pupæ after the third day the whole shell must be removed.

I have found collodionising the sections advantageous in young pupæ. This is easily effected by painting the cut surface of the paraffin block with thin collodion, which dries almost instantaneously.

As the study of the development in the egg and pupa necessitates the preparation of a large number of sections, the process of staining these after they are cut, although it gives the best results, is far too laborious; it is necessary, therefore, to have a good method of staining *en masse*.

The best method is Lang's picro-carminic and eosin.\* The eosin in some way acts as a carrier for the carminic, and is afterwards washed out with 70 per cent., and then with absolute alcohol.

It is impossible to over-stain, and the nymph should be left from four days to a week in the stain.

My friend, Brigade-Surgeon Scriven, has been indefatigable in preparing serial sections of nymphs, which he has very kindly placed at my disposal, and he adopts the above method most frequently. His specimens are very beautiful and definite, and I take the present opportunity of thanking him for his valuable assistance.

Viallanes used collodion as a material for imbedding the nymph, and I have obtained very fair results from its use. I am not, however, prepared to recommend it for serial sections, and I have not found it to possess any advantages over paraffin. When celloidin or collodion are used, either for imbedding, or for collodionising paraffin sections, oil of cloves should not be used as a clearing agent. Equal parts of xylol and solid carbolic acid may be employed instead, but the slides must be well washed with xylol to remove all traces of carbolic acid before they are finally mounted with balsam.

The details of these processes and much valuable information on technique will be found in the second edition of the '*Microtomist's Vade-Mecum*,'† which is a far better work than the first edition, from which I formerly quoted.

The outer covering of the pupa or embryo is easily removed with a little practice. Perhaps the best method is to cement the eggs or pupæ to a slide with gum or shellac in creasote; the outer covering can then be cut with a sharp needle, and the embryo or nymph removed. This must be done under dilute alcohol—50 per cent. is sufficient—with a dissecting microscope.

\* Equal parts of a solution of picro-carminic, Weigert's or Ranvier's, and a 2 per cent. aqueous solution of eosin.

† '*The Microtomist's Vade-Mecum*,' by A. Bolles Lee, second edition, London, 1890.

I then make a drawing of the external form of the embryo or nymph, which is subsequently a great aid in the interpretation of sections, and transfer the preparation to 75 per cent., and after an hour or two to absolute alcohol.

In a week or ten days the preparation should be transferred to the staining solution. I think it is advantageous to place specimens intended to be stained with picro-carmin in a solution of picric acid in 50 per cent. alcohol for a few days, before transferring them to alcohol.

In preparing sections of the imago, it is necessary to cut the insect into two or more parts, or to remove a portion of the integument, and then to fix the tissues either in absolute alcohol with ten to twenty drops of a solution of osmic acid to half an ounce of alcohol, or to place them in a solution of picric acid in 75 per cent. alcohol. Fixation by heat is inadmissible, as the tracheæ swell and displace and vacuolate all the tissues. It is most important to bear in mind that specimens hardened in picric acid must never be wetted with water subsequently.

I have not found that such dilute osmic solution as I have recommended prevents subsequent staining with hæmatoxylin.

For logwood-staining after cutting, I consider Müller's fluid far the best fixative for imagos. A week or ten days is sufficient before transferring to alcohol. Such specimens must be washed in large quantities of dilute alcohol, 50 per cent., to remove the chromates.

Whenever it is possible, young imagos should be used, as the chitin of the adult is most difficult to cut. I have, however, succeeded in cutting egg-bearing females without serious fracture of the integument. To do this it is necessary to be very careful that the temperature of the paraffin used for imbedding does not rise even for a few minutes much above its melting-point, and any such rise of temperature is always most destructive. Neither must the insects be kept in absolute alcohol more than a few days previously. Such insects should, I think, always be fixed with Müller's fluid. I have found eau-de-Javelle and eau-de-Labarraque, so much extolled, exceedingly destructive to the internal organs, so that they are quite inadmissible.

The rapid fixation of the tissues of the imago, so essential to good results, can only be insured by first washing the whole insect in alcohol to remove the waxy secretion from the integument, unless absolute alcohol is used as a fixative. An exhausting syringe is useful to assist the permeation of the insect by the fixative fluid, but, if alcohol be used for washing, is not essential; indeed, of late years I have not used it.

Benzoline has recently been recommended as a substitute for chloroform before imbedding in paraffin. I cannot, however, recommend it, as I am sure it is more destructive to the tissues than chloroform. It has also been recommended instead of turpentine for removing the paraffin from sections. It certainly does so more rapidly, but I consider its use dangerous, and, although cheaper than turpentine, I do not think it should be employed. Xylol is equally dangerous, as its vapour is most inflammable. When used, it ought to be kept in a small bottle, and employed with great caution. A serious accident may readily occur from any carelessness.





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